Neural Correlates of Subjective Familiarity and Choice Bias during Episodic Memory Judgments

Neural Correlates of Subjective Familiarity and

Choice Bias During Episodic Memory Judgments

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Abstract

Successful recognition memory decisions depend on mnemonic and decision making processes that are computed by multiple, distributed brain areas. However, little is known about what computations these areas perform or how these areas are connected. Here, I collected behavioral and functional magnetic resonance imaging data from humans during the performance of an old-new recognition memory task with retrospective confidence judgments. Across runs, choice bias was successfully manipulated by providing rewards for correct responses that were either symmetric (equal reward for hits and correct rejections) or asymmetric (one response worth more than the other). Successful recognition memory was associated with activation in anterior prefrontal, parahippocampal, posterior cingulate, and parietal cortex. Resting state functional connectivity demonstrated that these brain areas are organized into two distinct networks. The first network includes parahippocampal cortex and angular gyrus. The second network includes lateral prefrontal cortex and intraparietal sulcus. The hippocampal-cortical network was most active during old vs. new decisions, did not differentiate hits from false alarms, and was differentially active during low confidence old and new judgments. In contrast, while the frontoparietal network was robustly activated by hits, it was not activated during either false alarms or low confidence old judgments. Thus, these two distinct networks

can be distinguished by their relative connectivity to the medial temporal lobe vs. lateral prefrontal cortex and their responses during uncertain old judgments and errors. The choice bias manipulation had opposing effects on the parietal components of these networks, which further suggests these networks make distinct contributions to mnemonic decision making.

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Introduction

As is represented in most models of mnemonic decision making (e.g. signal detection or diffusion models), recognition memory judgments rely on both mnemonic and decision making processes. In the standard yes-no memory recognition task, participants discriminate between studied and unstudied memory probes. Studied probes (target items) are presumed to produce normally distributed internal signals (neuronal activation) that vary in magnitude along a dimension of familiarity, mnemonic strength, or item relatedness. Non-studied probes (lure items) are presumed to result in familiarity signals that are similarly distributed, but with a reduced overall mean and standard deviation due to relative novelty. Accurate memory recognition relies on discriminating target items that lead to internal memory-related activation (signal+noise) from lure items that are associated with weaker memory-related activation (noise).

When judgments must be made in the absence of perfect discriminability (i.e. overlapping signal and noise probability distributions), motivated individuals must commit to a decision in the presence of uncertainty. Other sources of relevant information, such as emotional valence, priors, or the estimated value of a choice, will have increasing significance as the decision making process becomes more uncertain. Signal detection models assume that participants make old-new decisions by comparing the evoked mnemonic strength of a test probe with an internal decision criterion or threshold (e.g. Green and Swets, 1966; Hockley and Murdock, 1987; Snodgrass and Corwin, 1988). In signal detection theory, the difference in familiarity evoked by targets or lures is defined as discriminability and the location of the decision criterion relative to lure and target familiarity distributions is defined as the choice bias. Similarly, diffusion models of memory recognition assume old-new decisions are reached by comparing an internal decision criterion with the summation of baseline biases and accumulated mnemonic evidence or

familiarity (e.g. Ratcliff, 1978; Ratcliff and McKoon, 2008; Rorie et al., 2010). Empirical research has suggested that discriminability is invariant to explicit manipulations of choice bias and vice versa (Snodgrass and Corwin, 1988). Thus, to understand the neuronal mechanisms underlying recognition memory judgments, one must study the potentially independent contributions of mnemonic and biasing information to the decision making processes.

Neuroimaging tools, including event-related potentials (ERP) and functional magnetic resonance imaging (fMRI) have been extensively used to explore the neural substrates of memory recognition memory decisions (for reviews see Buckner and Wheeler, 2001; Rugg and Henson, 2002; Wagner et al., 2005; Skinner and Fernandez, 2007; Ciaramelli et al., 2008; Cabeza et al., 2008; Vilberg and Rugg, 2008). Memory recognition engages over a dozen brain regions including areas in or around the medial prefrontal, lateral anterior prefrontal, superior frontal, posterior parietal, intraparietal sulcus, retrosplenial and posterior cingulate, precuneus, posterior parahippocampal cortex, hippocampus, and lateral temporal cortex. Of all these brain regions, the role of the lateral parietal cortex in episodic memory has become the focus of increased scrutiny because of its consistently reported involvement during retrieval success and recollection (Wagner et al., 2005; Cabeza et al., 2008; Vilberg and Rugg, 2008) as well as its anatomical and functional connections with the medial temporal lobe (Cavada and Goldman-Rakic, 1989; Kobayashi and Amaral, 2003; Lavenex et al., 2002; Suzuki and Amaral, 1994; Rockland and Van Hoesen 1999; Clower et al. 2001; Blatt et al., 2003; Vincent et al., 2006; Kahn et al., 2008). The precise role of parietal cortex in memory recognition remains unclear. However, recent data suggest that parietal cortex may play a role in the representation of the subjective strength or content of memory (Vilberg and Rugg, 2007; 2009b; Shannon and

Buckner 2004) and/or adaptive biasing during decision making (Herron et al., 2004; Curran et al., 2007; O'Connor et al., 2010; Dobbins et al., 2012).

Current Theories for Recognition Memory Decision Making

Recently, several hypotheses have been proposed to account for activity modulations in parietal cortex during decision making. Below, I briefly review the predictions made by three prominent hypotheses of parietal involvement in memory recognition decision making.

Retrieval Theory

Retrieval theory is a dynamic signal detection model that uses sequential analysis to represent a decision as the noisy process that accumulates evidence over time from an initial starting point to a decision criterion (Ratcliff, 1978; Gold and Shadlen, 2007). According to retrieval theory, evidence in favor of a decision is integrated over a fixed deliberation time and stored as a decision variable or mnemonic accumulator (Ratcliff, 1978; Shadlen and Newsome, 2001; Gold and Shadlen, 2007; Wagner et al., 2005). In addition to evidence, a decision variable can be adjusted by statistical knowledge (such as likelihoods or priors) and subjective inclinations (such as reward value or emotional valence) (Ratcliff, 1978; Shadlen and Newsome, 2001; Gold and Shadlen, 2007). The internal goals of the subject set a decision rule that specifies how much activation is required to reach the criterion for a decision. The function of a decision variable is to achieve the participant's goal, which could include maximizing speed, accuracy, reward, or any other goal. In the context of a memory recognition task, retrieval theory proposes that the magnitude of activation in the decision variable represents the amount of support or opposition to the potential choice (e.g. old or new judgment). A decision rule is applied such

that a response is initiated if the evidence that a probe is old reaches the criterion. Retrieval theory operationalizes choice bias as a parameter affecting the distance between the starting point and the criterion for a decision (Ratcliff, 1978; Rorie et al., 2010). Deliberation is operationalized by the process of accumulating all sources of critical information about the decision. Therefore, the brain region that represents the decision variable will be late in the functional hierarchy of areas engaged during recognition memory decisions. Candidate decision variables often include brain regions associated with motor planning such as posterior parietal and premotor cortex (Shadlen and Newsome, 2001; Romo et al., 2004, Heekeren et al., 2004).

Recently, it has been proposed that parietal cortex may function as a mnemonic accumulator and perhaps a decision variable (Wagner et al, 2005). The primary difference between a mnemonic accumulator and a decision variable is that a decision variable would be influenced by non-mnemonic information relevant to the memory decision (e.g. priors or rewards). Retrieval theory makes three predictions about a mnemonic decision variable. First, a mnemonic decision variable will correlate with the subject's decision and therefore must be activated by both hits and false alarms, but not correct rejections or misses. In general, a mnemonic accumulator will have a similar activation profile as a decision variable. However, a decision variable and a mnemonic accumulator are predicted to dissociate in the context of a strong choice bias. Second, a mnemonic decision variable and a mnemonic accumulator must correlate with the strength of the evidence in favor of an old judgment. Third, since a decision variable incorporates relevant non-mnemonic sources of information, the mnemonic decision variable (but not a mnemonic accumulator) must correlate with shifts in choice bias induced by statistical knowledge or rewards. More specifically, factors that induce a liberal response criterion are expected to lead to more activation in the decision variable, and factors that induce a

conservative criterion are predicted to reduce activation in the decision variable. The effect of choice bias on activation is more easily measured on lure (vs. target) trials because mnemonic evidence is presumably held constant.

Dual-Process Theory

Dual process theory proposes that two qualitatively distinct retrieval processes are implemented by distinct anatomical memory systems (Mandler, 1980; Brown and Aggleton, 2001; Yonelinas, 2002; Vilberg and Rugg, 2008; Eichenbaum et al., 2007, but see Wais et al., 2006; Squire et al., 2007). The familiarity process computes a quantitative index of familiarity or mnemonic strength that may be modeled with an equal variance signal detection model. A second recollection process is an all-or-none process that is engaged when specific contextual associations of the past experience are remembered. Support for the dual process theory comes from process dissociation procedure (Jacoby, 1991), the remember-know procedure (Tulving, 1985), and analysis of the shape of receiver operating characteristic (ROC) curves (Yonelinas and Parks, 2007). An ROC curve is commonly obtained by plotting the hit rate vs. the false alarm rate as a function of retrospective confidence judgments. ROC curves have a bowed shape that can be used to measure mnemonic sensitivity. Behavioral manipulations that increase familiarity have been shown to increase the bowing of the ROC curve, but not the asymmetry (Yonelinas and Parks, 2007). In addition, ROC curves are frequently asymmetric, which reflects greater accuracy for high confidence judgments. Behavioral manipulations that increase recollection have been shown to selectively increase the asymmetry (but not the bowing) of the ROC curve (Yonelinas and Parks, 2007).

Recently, it has been proposed that posterior, inferior parietal cortex may play a significant role in recollective processing (Vilberg and Rugg, 2008). More specifically, it has been hypothesized that parietal cortex may function as an episodic buffer that holds recollected information in a form accessible to working memory (Baddeley, 2000; Wagner et al., 2005; Vilberg and Rugg, 2008). Dual process theory makes several predications about patterns of brain activation during recognition judgments. First, recollected items will result in more high confidence old judgments than items judged to be old on the basis of familiarity (Yonelinas, 2001). Critically, activation within a brain region that supports the process of recollection is not expected differ between correct rejections, misses, and low confidence old judgments that are presumably made based on familiarity. Thus, the contrast of low confidence hits vs. correct rejections is expected to yield a null result in regions underlying recollection processes. Second, a brain region that supports recollection should not be engaged during false alarms, which are unlikely to be accompanied by recollected mental content (such as images or sounds or other remembered associations). With some exceptions (e.g. Deese, 1959; Roediger and McDermott, 1995), false alarms are associated with low confidence and made on the basis of weak familiarity signals. Similarly, adjustments to the criterion should only influence familiarity-based recognition responses because the dual-process theory assumes that recollection is unaffected by choice bias (Yonelinas et al., 1999). Third, activation within a brain region that supports familiarity is expected to show a positive or negative correlation with variables that correlate with subjective memory strength, such as retrospective confidence judgments (e.g. Yonelinas et al., 2005; Daselaar et al., 2006).

Attention to Memory

The attention to memory theory (AtoM) is adapted from theories of visual attention (e.g. Corbetta and Shulman, 2002) and proposes that the parietal lobe is involved in both top-down and bottom-up attention to memory (Wagner et al., 2005; Cabeza, 2008; Ciaramelli et al., 2008). The AtoM theory contains two distinct sets of hypotheses that must be considered and evaluated separately. The first part of the AtoM theory posits that dorsal parietal cortex specializes in top-down control of mnemonic attention and guides retrieval according to goals or expectations. Evidence for this view comes from neuroimaging studies that demonstrated that activation in parietal cortex is modulated by priors (Herron et. al., 2003; Herron et al., 2004; Vilberg and Rugg, 2009a; O'Connor et al., 2010). For example, Rugg and collaborators manipulated the ratio of targets and lures in the retrieval test and found that the retrieval success effect in parietal cortex interacted with target-lure ratio (Herron et. al., 2003; Herron et al., 2004; Vilberg and Rugg, 2009a). Similarly, O'Connor and colleagues (2010) presented anticipatory cues that indicated the possible status of an upcoming probe (lure or target). When expectations were violated, they observed robust activation in parietal cortex. Furthermore, recent evidence suggests that patients with parietal lesions fail to incorporate priors or informative cues into their mnemonic decisions (Dobbins et al., 2012; Ciaramelli et al., 2010). The second part of the AtoM theory proposes that ventral parietal cortex is engaged by bottom-up captured of mnemonic attention triggered by spontaneous retrieval processes. Evidence that ventral parietal cortex is engaged in bottom-up capture of attention comes from neuroimaging studies that report parietal activation associated with recollection (Cabeza et al., 2008) and reports that patients with parietal lesions have impairments in spontaneous (but not cued) autobiographical recall (Berryhill et al., 2007). More specifically, patients with lateral parietal lesions recall memories with fewer details

and reduced vividness relative to controls. (Berryhill et al., 2007; Davidson et al., 2008). However, when no differences between patients and controls were found.

The top-down AtoM theory makes several predictions about brain activity in parietal cortex. First, dorsal parietal cortex (but not ventral parietal cortex) will be more activated when participants receive instructions or cues intended adjust choice bias or retrieval goals. Second, dorsal parietal cortex will be modulated by factors that induce changes in decision criteria (e.g. priors, value) and will correlate with shifts in response criteria. Factors that induce a liberal response criterion are expected to increase activation dorsal parietal cortex; factors that induce a conservative criterion are predicted to reduce activation (e.g. Rorie et al., 2010). Third, activation in ventral parietal cortex will be activated when the subjective familiarity of a probe overrides preexisting biases or expectations. Therefore, ventral parietal cortex will be most activated during old judgments that occur in the context of a conservative choice bias. The second and third predictions suggest an interaction between dorsal and ventral parietal cortex such that greater activation in ventral parietal cortex is required for an old decision in the presence of an induced conservative response criterion represented by dorsal parietal cortex.

Description of the Project

The aim of the experiment was to identify brain regions that support mnemonic decision making and document how those regions respond to recognition memory errors, subjective familiarity strength, and choice bias induced by payoffs. At retrieval, reward contingencies for correct old or new responses were varied to promote liberal, neutral, and conservative choice bias. An explicit manipulation of mnemonic strength was not conducted. However, mnemonic strength was estimated by asking participants to make a retrospective confidence rating for each

categorical old-new decision. Confidence ratings were made on a 6-point scale ranging from 1 = high confidence new to 6 = high confidence old.

To reduce the number of comparisons, hypotheses about parietal cortex were tested using a region of interest approach. Several recent reviews highlight functional dissociations between dorsal and ventral parietal cortex during memory recognition (Wagner et al., 2005; Vilberg and Rugg, 2008; Cabeza et al., 2008). However, it is challenging to compare results across studies due to the complexity of parietal cortex and variability in atlas registration procedures. Recently, it has been proposed that spontaneous fluctuations in neural activity are characterized by consistent patterns of interregional covariance that can be used to for functional localization and the study of comparative anatomy (Biswal et al., 1995; Fox and Raichle, 2007; Buckner and Vincent, 2007). Critical to the goals of the present study, a consistent schema for parcellating the parietal lobe has begun to emerge (Vincent et al., 2008; Nelson et al., 2010; Yeo et al., 2011; Lee et al., 2012). In particular, two of these large-scale functional networks have been proposed to participate in long-term memory retrieval (see Vincent et al., 2008 for discussion). The first network includes the inferior parietal lobule, hippocampus, parahippocampal, retrosplenial, posterior cingulate, and ventral medial prefrontal cortex (Greicius et al., 2004; Vincent et al., 2006). The second network includes intraparietal sulcus, anterior prefrontal, dorsolateral prefrontal, anterior cingulate, and lateral temporal cortex (Vincent et al., 2008; Spreng et al., 2010). Recent studies suggest that the spontaneous correlation mapping technique is an effective method of targeting brain regions responsive during recognition memory judgments (Vincent et al., 2006; O'Connor et al., 2010). Therefore, I identified the parietal components of these networks as *a priori* regions of interest for all major statistical comparisons.

Materials and Methods

Participants

In this study, I acquired fMRI and behavioral data from 44 healthy native English-speaking participants. Data from 32 participants (12 males, 20.9 ± 2.9 years old, ranged from 18 to 30) were included in the analysis of task-performance and task-based functional neuroimaging. Task data from the remaining participants were excluded due to claustrophobia (N = 1), failure to distribute responses across all six levels of confidence (N = 3), behavioral performance outlier (N = 1), or technical difficulties during fMRI data acquisition (N = 2). During data collection, a mistake was made in run counterbalancing that led to the exclusion of five participants. Resting state data were available for ten of the participants excluded from the task analyses and was used as an independent supplementary resting state data set for the region of interest generation. All participants had normal or corrected-to-normal vision and were right handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). No participant reported any neurological or psychiatric history. Each participant gave informed consent according to a procedure approved by the Committee on the Use of Human Subjects at Harvard University. Participants received an incentive-compatible payment of approximately $100 (mean = 98.66; range $90-$109).

Experimental Design

Participants performed an abstract-concrete encoding task that was followed by an old-new recognition memory task (similar to Demb et al., 1995). An overview of the experimental design for the old-new memory recognition task is presented in Figure 1. For each recognition memory trial, participants simultaneously judged whether or not the presented item was old or

new and indicated whether they had low (LC), medium (MC), or high confidence (HC) in their decision (similar to Daselaar et al., 2006). These retrospective confidence ratings provide an estimate of subjective familiarity of an item on a 6-point scale. At the beginning of each recognition memory trial, participants were presented with two cues that indicated how much money an accurate old or new decision would be worth (similar to Rorie et al., 2010). The cues were ¢ signs or $ dollar signs, which indicated low and high rewards, respectively. The left/right placement of the cues on the screen was always congruent with the associated left/right hand responses for either old or new decisions. The amount of money that could be received for a correct response, however, changed for each functional run. During some runs, an accurate old response was worth the same as an accurate new response. During other runs, an accurate new response was worth more than an accurate old response or vice versa. The reward contingency cues were designed to induce a conservative, neutral, or liberal choice bias in participant behavior. The main goal of this experiment is to identify brain regions with activity that correlates with subjective mnemonic strength, choice bias, or both variables.

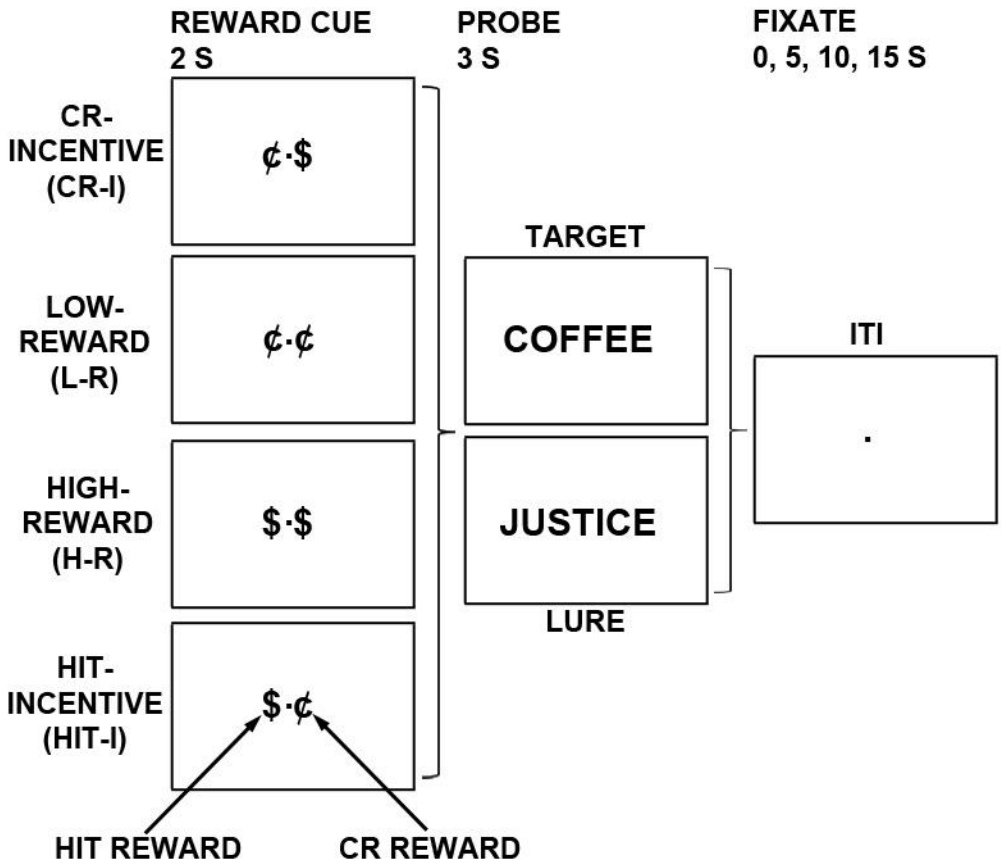


Figure 1. Recognition memory paradigm with variable reward contingencies. Trials begin with a 2 s presentation of pair of cues that indicated the reward value of an accurate old or new judgment to an upcoming probe. A ¢ cue indicated a low magnitude reward, while a $ indicated a high magnitude reward. In the figure, the reward for hits is shown on the left of the fixation point and the reward for correct rejections (CRs) is shown on the right of the fixation point. The left/right placement of the cues varied across participants, but was consistent within participants. The cues associated with each of the four reward conditions are presented vertically on the left. Following the offset of the cue, a probe appeared for 3 s, and participants made a single button press response to simultaneously indicate whether the probe was old or new and how confident they were in their judgment. Each trial was followed by a variable inter-trial interval (ITI).

Task Specification

Stimuli

Stimuli were 448 high-frequency words (length: mean 6.72, range 4-8 letters; Hyperspace Analogue to Language (HAL) log frequency: mean 6.11, range 5.00-6.99) taken

from the English Lexicon Project (Balota et al., 2007; http://elexicon.wustl.edu). The words were randomly divided into 16 sets of 28 words that were rotated across reward contingencies, target-lure status, and participants.

During the recognition phase, all stimuli were centrally presented in upper case letters using an Apple Macbook Pro (Apple Computers, Cupertino, CA) and projected (Sharp XG-C465X) onto a DA-100 screen (DA-Lite, Warsaw, IN) located approximately 87 cm away from participants eyes at the head of the magnet bore (max horizontal visual subtense 5.3°; max vertical visual subtense 1°). Participants viewed the screen using a mirror attached to the head coil. All stimuli were presented in black against a white background. A fixation point was continuously present at the center of the screen except when words were presented. Responses were recorded on a custom button keypad using Psychophysics Toolbox Version 3 (www.psychtoolbox.org) and Matlab (Version 7.9.0, 2009b, Mathworks).

Behavioral Procedure

The study consisted of an encoding phase conducted outside of the scanner and a recognition phase within the scanner. During the encoding phase, participants were seated alone in a room facing a monitor with the index fingers of both hands resting on response keyboard. For the recognition phase, participants were placed in an MRI scanner with the index, middle and ring fingers of each hand positioned over buttons on response keypads. Response key assignments for both the encoding and recognition tasks were counterbalanced across participants. The participants had instructions read to them and explained verbally prior to the start of both the encoding and recognition experiment. (Written instructions for encoding and recognition are included in Appendix 2A and 2B, respectively.) Before data collection,

participants practiced the recognition task until the task was understood and accuracy was greater than 85% correct.

Encoding phase trials consisted of abstract-concrete judgments on a sequence of 224 words presented centrally for 2 s. Participants indicated with either a left or right hand index finger key press whether the study word was an abstract or concrete noun. Concrete nouns were defined as anything that could be seen, heard, smelled, tasted, or felt such as "dog" or "table". Abstract nouns were defined as something one cannot experience with the senses, such as "intelligence" or "liberty." Prior to each encoding block, participants were reminded of which key corresponded to which response. Participants were instructed to respond as quickly as possible without sacrificing accuracy. Before the beginning of the encoding phase, participants conducted short practice sessions to ensure they understood the task. The encoding phase was administered in 8 successive sessions of 56 s each. There was a delay of approximately one hour between encoding and the recognition memory test.

Figure 1 illustrates the sequence of events in the recognition task. Recognition test trials were 5 s long. The trial began with a 2 s cue indicating the magnitude of reward available to the participant for correctly responding either old or new. Following the cue, a probe was displayed for 3 s, to which the participant was required to make an old-new judgment. Recognition probes included all 224 target words included in the abstract-concrete encoding task intermixed in equal ratios with 224 lure words not seen in the abstract-concrete task. In addition, 272 fixation-only trials ("null events") were interspersed among recognition trials to facilitate modeling the hemodynamic response to recognition trials. The order of trial types were arranged pseudo-randomly to allow for hemodynamic signal extraction (Dale and Buckner, 1997).

Cues indicating reward value contingencies were presented before each recognition memory judgment to encourage a value-induced choice bias in behavioral performance. During the cue phase, there were two potential reward values for a correct response: a high reward (40¢) and a low reward (16¢). Importantly, participants were not told the exact value of the reward. The low reward was described as "a few pennies," and the high reward was characterized as "a larger cash value." Participants received an incentive compatible payment determined by behavioral performance with the exception that no participant was compensated less than $90 or more than $110. There were four types of reward value cues: correct rejection-incentive cues (CR-I, low reward for a hit; high reward for a correct rejection, CR), Low-Reward cues (L-R, low reward for a hit or CR), High-Reward cues (H-R, high reward for a hit or CR), and hit-incentive cues (HIT-I, high reward for a hit; low reward for a CR). Participants were told that they would not receive any reward for incorrect responses. In addition to the reward value cue, the recognition task instructions also encouraged a choice bias. Participants were told, "The majority of the money you will be making from the experiment today will be from accurate responses to items with high reward values. Therefore, you don't want to not miss a high reward item."

Immediately following the cue, either a target or a lure was presented centrally for 3 s. For each word, participants were instructed to press one of six buttons to indicate simultaneously 1) whether they remember that word as having been presented during the encoding phase and 2) how confident they were in their judgment. Responses were given with the index, middle, and ring fingers of the left and right hands. Half of the participants were asked to make a left hand response if the word was previously studied (i.e. old) and a right hand response if the word was not previously studied (i.e. new). For the other half, this response assignment was reversed. For

each old/new judgment, participants were asked to respond with different fingers depending on their confidence in their judgment. Specifically, they were asked to respond with 1) the index finger if they were unsure of their choice, were guessing, or otherwise had low confidence in their judgment, 2) the middle finger if they were reasonably sure or had moderate confidence in their judgment, and 3) the ring finger if they felt certain and had high confidence in their judgment. Each participant performed practice sessions until they were comfortable with the task, including the reward cues and response mappings. In addition, the response mapping was presented visually on the screen as a reminder before each block of trials began. Prior to each recognition block, participants were verbally and visually instructed of the upcoming reward contingencies as well as which key corresponded to which response. Participants were asked to respond quickly and accurately.

The recognition memory test was approximately 70 minutes long and was divided over eight fMRI runs of 7.5 minutes each. Each run contained only one type of reward contingency cue, and run order was counterbalanced across participants. All subjects in the analyses completed eight 7.5-minute runs of 56 recognition memory trials (2 runs for each reward cue condition). Two runs from one of the subjects were removed due to stimulus timing synchronization failures (1 L-R, 1 H-R). After completion of the experiment, participants were debriefed about the motivation for the study.

Behavioral Analysis

Trials with response times below 400 ms were discarded from all analyses. Behavioral data were analyzed according to the signal detection theory.

Discriminability d' was estimated as:

$$d' = Z_{hit} - Z_{fa},$$

where Z_{hit} and Z_{fa} are the standard scores for hit and false alarm rates. The value *d'* cannot be calculated when there are hit rates of 1 or false alarm rates of 0. Therefore, both hit and false alarm rates were adjusted by adding 0.5 to each frequency and dividing by N + 1, where N is the number of target or lure items (Snodgrass and Corwin, 1988).

Choice bias was estimated using the criterion location measure (Macmillan and Creelman, 2005):

$$C = -\frac{1}{2}\left(Z_{hit} + Z_{fa}\right)$$

Positive values of *C* indicate a conservative choice bias while negative values indicate a liberal choice bias.

A receiver operating characteristic (ROC) curve is obtained by plotting the hit rate vs. the false alarm rate as a function of criterion setting. Empirical ROC curves were obtained by using the five criterion settings associated with the six retrospective confidence ratings. zROC curves were obtained by transforming the hit and false alarm rates to standard Z-scores. The theoretical definition of standard scores is as follows:

$$Z_{hit} = -\left(\frac{C-\mu_T}{\sigma_T}\right),$$

$$Z_{fa} = -\left(\frac{C-\mu_L}{\sigma_L}\right),$$

where μ_T and μ_L are the means and σ_T and σ_L are the standard deviations for the target and lure distributions, respectively. The above equations for standard scores estimate the area under the curve for the relevant distribution from the criterion location, *C*, to infinity.

By combining the two above equations for standard scores, it can be proven that the slope of the zROC curve provides an estimate of the ratio of the variance of the lure distribution to the variance to the target distribution (Egan, 1958; Ratcliff et al., 1992).

$$z_{hit} = \frac{\sigma_L}{\sigma_T} z_{fa} + \frac{\mu_T - \mu_L}{\sigma_T}$$

By assuming normal distributions for lures and targets and assigning the lure distribution zero mean and unit variance, I estimated the relative mean and variance of the target distribution using the zROC curve. This method formed the basis for empirically estimating the signal detection theory gaussians presented in Figures 4 and 5.

MRI Data Acquisition

Functional imaging was conducted on a 3 T Tim Trio MRI system (Siemens, Erlangen, Germany) using the vendor-supplied 12-channel phased-array head coil at the Center for Brain Science at Harvard University. The functional imaging data were acquired using a gradient-echo echo-planar imaging (EPI) sequence sensitive to blood oxygenation level-dependent (BOLD) contrast (Kwong et al., 1992; Ogawa et al., 1992). Ten functional runs (8 memory task runs and 2 resting state runs) were collected from each participant that completed the study. Whole brain coverage was achieved with slices aligned to the anterior commissure-posterior commissure plane using an automated alignment procedure that ensured consistent acquisition across participants (van der Kouwe et al., 2005). Structural data included a high-resolution multiecho T1-weighted magnetization-prepared gradient-echo image (multiecho MP-RAGE; van der Kouwe et al., 2008).

For the eight memory task performance scans, EPI parameters were as follows: repetition time (TR) = 2500 ms, echo time (TE) = 30 ms, flip angle (FA) = 85°, 3 × 3 × 3 mm voxel resolution, field of view (FoV) = 216, and 39 axial slices collected with interleaved acquisition and no gap between slices. Each task functional run lasted 7.5 min (180 time points). During resting state scans, participants were instructed to remain still, stay awake, and keep their eyes open. Resting state scan EPI parameters were as follows: TR = 3000 ms, TE = 30 ms, FA = 85°, 3 × 3 × 3 mm voxel resolution, FoV = 216, and 47 axial slices collected with interleaved acquisition and no gap between slices. Each resting state functional run lasted 6.2 min (124 time points). Parameters for structural scans (MP-RAGE) were as follows: TR = 2200 ms, inversion time (TI) = 1100 ms, TE = 1.54 ms for *image 1* to 7.01 ms for *image 4*, FA = 7°, 1.2 ×1.2 ×1.2 mm voxel resolution, and FoV = 230. The multiecho MP-RAGE allows increased contrast through weighted averaging of the four derived images.

MRI Data Preprocessing

The fMRI data preprocessing included 1) discarding the first four volumes of each run to allow for T1-equalibration effects, 2) compensating for slice acquisition-dependent time shifts per volume with SPM2 (Wellcome Department of Cognitive Neurology, London, UK), and 3) correcting for head motion using rigid body translation and rotation with the FSL package (Jenkinson et al., 2002; Smith et al., 2004). Volumes were normalized to a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain (Evans et al., 1993) in the atlas space of Talairach and Tournoux (1988) and resampled to a voxel size of 2 mm^3. Prior to analysis, all functional volumes were spatially smoothed with a 6-mm full width at half-maximum (FWHM) Gaussian kernel.

The resting state data underwent further processing using the procedures adapted from Biswal et al. (1995) and optimized for functional correlation analysis (Fox et al., 2005; Vincent et al., 2006; Van Dijk et al., 2010). Briefly, constant offset and linear trend over each run were removed and a low-pass temporal filter was applied to retain frequencies below 0.08 Hz. Sources of spurious variance, along with their temporal derivatives, were reduced using linear regression. Estimates of spurious variance included six parameters of estimated volume displacement obtained by correction for rigid body head motion, the signal averaged over the whole brain, the signal averaged over the ventricles, and the signal averaged over the deep cerebral white matter. In this manner, variance unlikely to be involved in spatially specific regional correlations was removed from the data. The global (whole brain) signal may correlate with respiration-induced fMRI signal fluctuations (Birn et al. 2006; Wise et al. 2004; Van Dijk et al., 2010) or result from global fluctuations in neuronal activity. Removing signals correlated with ventricles and white matter is an additional means of reducing nonneuronal contributions to BOLD correlations (Bartels and Zeki, 2005; Fox et al., 2005).

fMRI Statistical Modeling

Analysis of the task performance fMRI data was completed using a general linear model as implemented in SPM8 (Wellcome Department of Cognitive Neurology, London, UK). Four reward cues and two probe types yielded a total of eight potential trial types (e.g. a hit-incentive cue followed by a lure). Three levels of retrospective confidence ratings and two categorical decisions about the probes allowed for six potential response types (e.g. low confidence old response). Multiple general linear models were estimated to fully explore the neural activity associated with each experimental condition and each type of response. Specifically, contrasts

were computed for each level of each independent variable (e.g. target/lure status), each level of each response type (e.g. old-new judgment), and each available combination of each level of each independent variable and each level of each response type (e.g. hit/miss or correct rejection/false alarm). Individual trials were modeled as events occurring at the onset of the cue (0 s duration). The BOLD effect for each behavioral condition was modeled in each voxel of the brain using a canonical hemodynamic function convolved with the event onsets times associated with behavioral conditions of interest. Separate regressors were constructed for each trial type and for trials without responses. Effects of interest and between-condition contrasts were generated at the individual subject (first) level. First level contrasts from each subject were then entered into ANOVAs and one-sample *t* tests to compute the group (second) level maps of statistical significance. All first level models included regressors of no interest that included six parameters of estimated volume displacement obtained by correction for rigid body head motion as well as the mean and linear trend computed for each run. Additional regressors were added for time points identified as extreme motion outliers (movements > 0.25 mm that were at least 5 s.d. from mean displacement within session). The fMRI time series was also high-pass filtered to remove frequencies less than 1/128 Hz.

Resting state functional connectivity maps were generated at the individual subject level by computing the Pearson product-moment correlation coefficient between a seed region of interest and all other voxels in the brain. For each subject, the correlation coeffients were coverted to *z* values using Fisher's *r*-to-*z* transformation (Zar, 1996). To assess significance at the group level, individual *z* maps were entered in to one-sample *t* tests as implemented in SPM8 (Wellcome Department of Cognitive Neurology, London, UK).

Whole brain effects were statistically thresholded at voxelwise uncorrected $P<0.001$. Stereotactic coordinates are reported in Talairach space and correspond to the standard MNI coordinate system (Evans et al., 1993). Activation maps were projected to the Caret PALS cortical surface (Van Essen et al., 2005) or overlaid onto the group-averaged MP-RAGE anatomy images in MNI space.

Hypothesis-driven regional analyses

I have previously demonstrated that coherent patterns of spontaneous activity are predictive of functional brain organization and can be utilized for functional localization in memory tasks (Vincent et al., 2006). Here, I seek to build on previous findings by once again defining *a priori* regions of interest (ROIs) from functional correlated networks that are known to be engaged during recognition memory judgments including the hippocampal-cortical network (Vincent et al., 2006; Kahn et al., 2008; Yeo et al., 2011) and the frontoparietal network (Vincent et al., 2008; Spreng et al., 2010; Yeo et al., 2011; Niendam et al., 2012). In particular, this method of defining regions is useful for the present goal of identifying distinct, but adjacent regions within parietal cortex for subsequent task analysis (e.g. O'Connor et al., 2010). Retrieval success is routinely associated with left lateralized activity regardless of whether the retrieval probes are words (Konishi et al., 2000; McDermott et al., 2000), faces (Leube et al., 2003), or sounds (Shannon and Buckner, 2004). For this reason, only regions from the left hemisphere were selected for the analysis of task activation. From the frontoparietal network, ROIs were selected within the anterior lateral intraparietal sulcus (alIPS) and the anterior prefrontal cortex (aPFC). From the hippocampal-cortical network, regions were selected from the posterior parahippocampal gyrus (pPHG) and the ventral-posterior inferior parietal lobule (vpIPL).

Table 1. Regions of Interest from Yeo, Krienen, et al., 2011

Region of Interest	Volume (cm^3)
posterior Parahippocampal Gyrus (pPHG)	2.39
ventral posterior Inferior Parietal Lobule (vpIPL)	1.07
anterior Prefrontal Cortex (aPFC)	5.60
anterior lateral Intraparietal Sulcus (alIPS)	2.91

Three sets of ROIs and two resting state data sets were employed in an iterative scheme to refine *a priori* ROIs for task analyses (for a similar strategy see Vincent et al., 2006; 2008; Kahn et al., 2008; Wig et al., 2013). The goal was to generate ROIs that would be the best guess of the mean anatomical location of each node in the network in the group of 32 subjects included in the task-based analyses. The initial set of volumetric ROIs were downloaded from the 17-network "tight" parcellation previously published by Yeo and colleagues (2011, see http://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation_Yeo2011). These ROIs were generated from a surface-based analyses and may not be appropriate for volume-based analyses. In addition, these four ROIs vary in volume between 1.07 cm^3 and 5.60 cm^3 (Table 1). Finally, due to variability in analysis procedures and individual anatomy, optimal ROIs would ideally be defined from resting state data collected from the subjects included in the task-based analyses. Despite these caveats, these ROIs provide a good approximation of the mean anatomical location

of prominent functional connectivity networks because the estimates were computed in 1,000 subjects.

Table 2. Regions of Interest from Supplementary Data Set

Regions of Interest	Volume (cm^3)	x	y	z
posterior Parahippocampal Gyrus (pPHG)	1.81	-16	-36	-14
ventral posterior Inferior Parietal Lobule (vpIPL)	1.74	-46	-72	32
anterior Prefrontal Cortex (aPFC)	2.07	-41	56	7
anterior lateral Intraparietal Sulcus (alIPS)	2.02	-49	-44	55

The first set of ROIs from Yeo, Krienen and colleagues (2011) were used to generate the functional correlation maps in the supplementary resting state data set (Figure 2). On the basis of function correlation maps in the supplementary resting state data set, two ROIs each were selected from hippocampal-cortical network and frontoparietal network (Figure 2, far right). From the frontoparietal network, regions were selected within the anterior intraparietal sulcus (alIPS) and the anterior prefrontal cortex (aPFC). From the hippocampal-cortical network, regions were selected from the posterior parahippocampal gyrus (pPHG) and the ventral-posterior inferior parietal lobule (vpIPL). This second set of ROIs were grown as spheres centered on peak coordinates (approximately 1.8 mm^3) and masked by the thresholded statistical map (Table 2). The second set of ROIs generated from functional correlation maps in the supplementary resting state data set were then carried forward as seed regions in the main data set of 32 subjects (Figure 3). From the functional connectivity maps in the main data set, a third set of refined ROIs were defined within alIPS, aPFC, vpIPL, and pPHG (Table 3). The

functional connectivity maps associated with the third set of ROIs are shown in Figure 6. These ROIs were approximately uniform in volume and obtained from the same subjects that were used in the task-based analyses. Therefore, these *a priori* ROIs were optimized for analysis of task-evoked activation.

Table 3. Regions of Interest for Task-Based Analyses

Regions of Interest	Volume (cm^3)	x	y	z
posterior Parahippocampal Gyrus (pPHG)	2.05	-26	-30	-24
ventral posterior Inferior Parietal Lobule (vpIPL)	1.70	-42	-78	32
anterior Prefrontal Cortex (aPFC)	2.05	-44	46	2
anterior lateral Intraparietal Sulcus (alIPS)	1.83	-46	-50	49

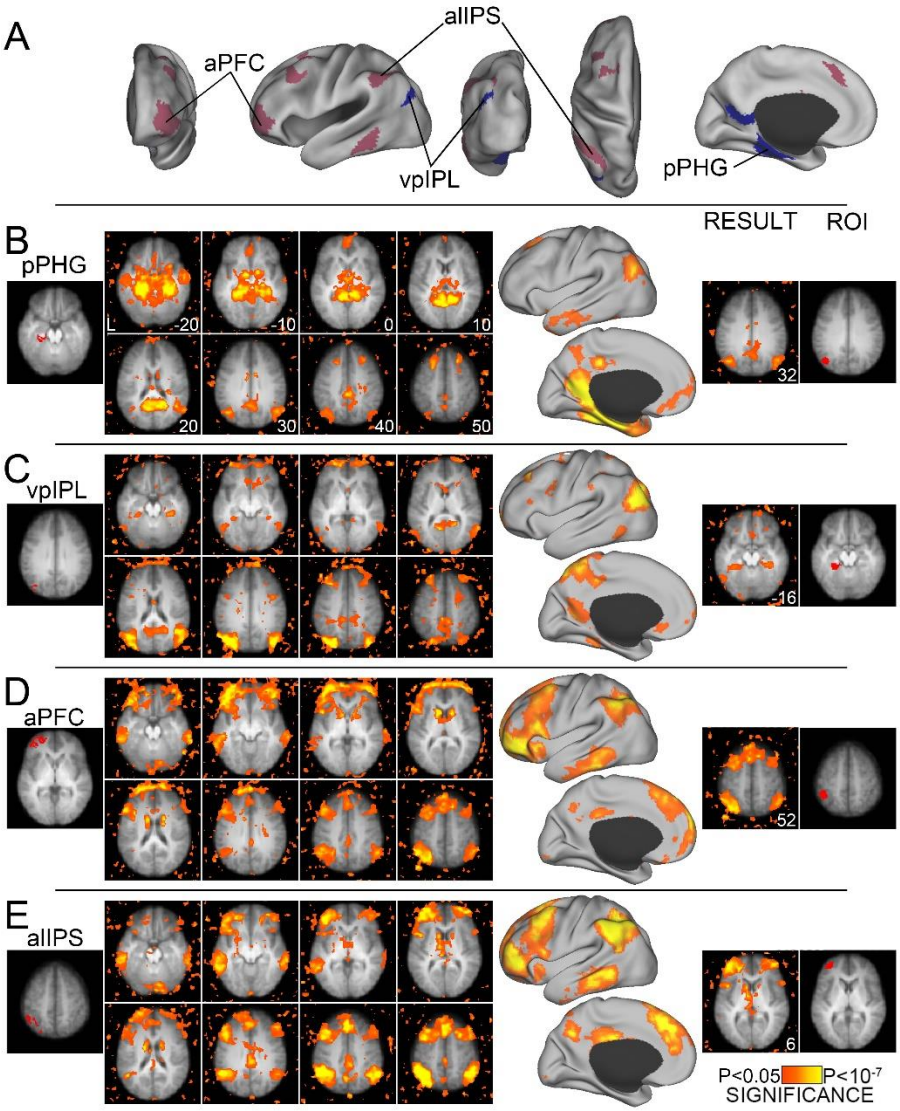


Figure 2. Significant spontaneous BOLD correlations in 10 humans (supplementary data set) associated with regions defined from the 17-network parcellation reported by Yeo and colleagues (2011). A) The maroon and dark blue networks that originated from a statistical parcellation of spontaneous BOLD fluctuations in the human cerebral cortex of 1,000 subjects (from Yeo et al., 2011). Regions of interest from this parcellation served as initial seed regions for this study. Selected regions include prominent components of the hippocampal-cortical system (dark blue network), including the posterior parahippocampal gyrus (**B**, pPHG) and ventral posterior inferior parietal lobule (**C**, vpIPL), as well as the frontoparietal system (maroon network), including the anterior prefrontal cortex (**D**, aPFC) and anterior lateral intraparietal sulcus (**E**, alIPS). Panels **B-E** display each of the seed regions as well as their associated functional connectivity maps. Seed regions are shown in red to the left. In the middle, each functional connectivity map is displayed as an overlay on the average subject anatomy and projected onto the Caret PALS cortical surface. Regions of interest that were selected from each functional connectivity map are shown on the right adjacent to a slice displaying the functional connectivity result. All functional connectivity maps are displayed as *t* statistics thresholded at $P < 0.05$ (uncorrected).

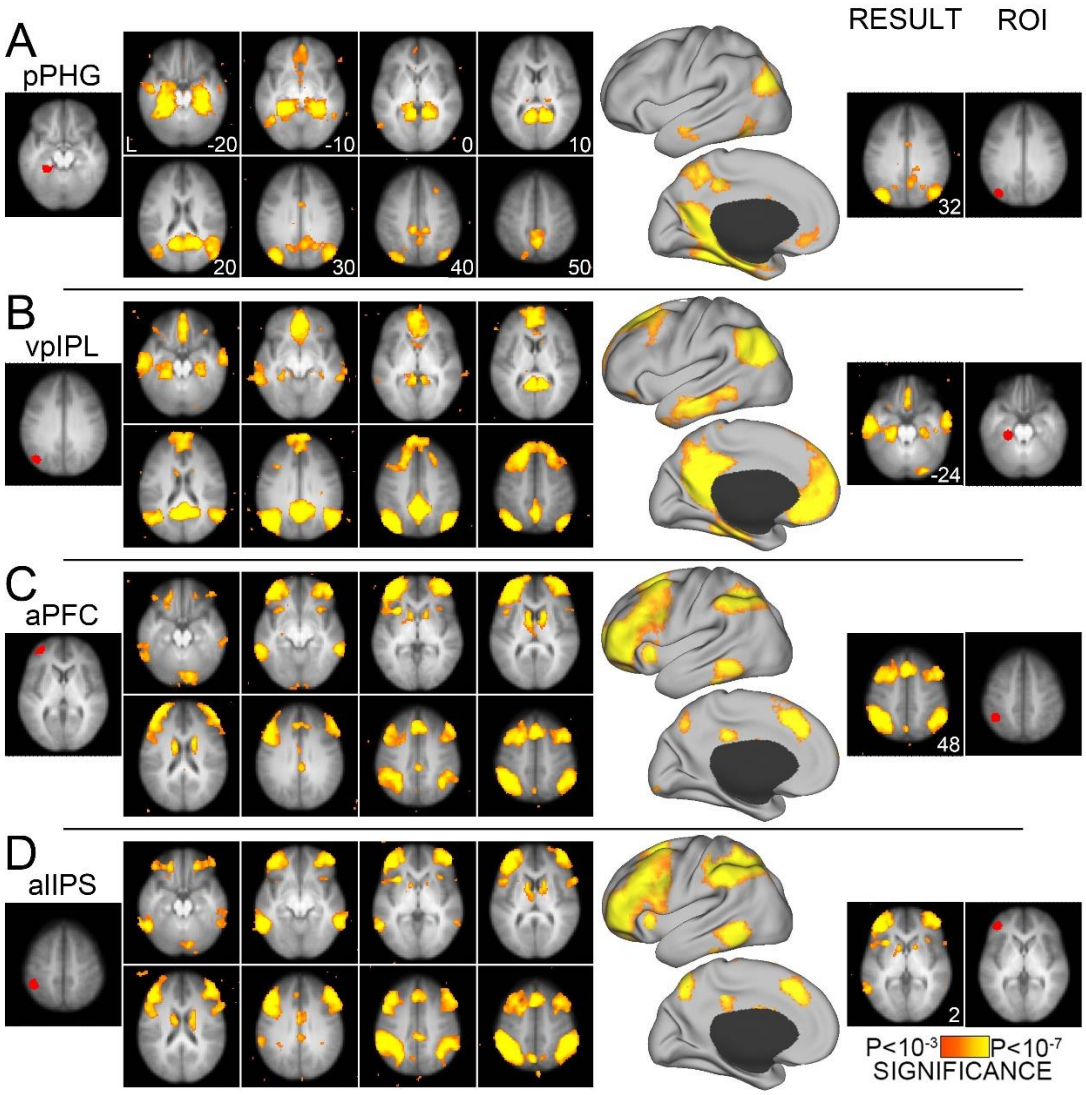


Figure 3. Significant spontaneous BOLD correlations in 32 humans (main data set) associated with seed regions defined from the supplementary data set (Figure 2, right). Seed regions include elements of the hippocampal-cortical system including parahippocampal gyrus (pPHG, **A)** and ventral posterior inferior parietal lobule (vpIPL, **B**), as well as the frontoparietal system, including the anterior prefrontal cortex (aPFC, **C**) and anterior lateral intraparietal sulcus (alIPS, **D**). All functional connectivity maps are displayed as *t* statistics thresholded at $P < 0.001$ (uncorrected). Format is similar to Figure 2.

Hypothesis-driven regional analyses of task activation were performed with *a priori* ROIs selected from functional connectivity analyses in the main resting state data set of 32 subjects (Figure 6). Magnitude estimates were calculated for each participant and each condition

and averaged within each ROI. This strategy represents a conservative approach to the problem of multiple comparisons, affords considerable power by averaging many voxels within a region, and provides an unbiased measurement of the size of an effect within a region (e.g. Buckner et al., 1995; Vincent et al., 2006). The effect of each task condition was estimated relative to an implicit baseline (passive fixation). Magnitude estimates for each participant were entered into a random-effects model and specific comparisons were made using ANOVAs and *t* tests.

Results

The abstract-concrete judgments were provided with a mean median response time of 1015 (139) ms.

Behavioral Results

Familiarity

Figure 4 shows group-averaged frequency, accuracy, and median response times as a function of judgment category (old, new) and retrospective confidence judgment (low, medium, high). A 2 × 3 repeated measures factorial ANOVA[1] revealed significant differences in the number responses subjects made for each potential response type. Old judgments were made more frequently than new judgments [$F(1, 31) = 19.30$ $P < 0.001$]. However, the response frequency did not vary by subjective confidence. In addition, there was an interaction between judgment category and confidence [$F(2, 62) = 29.50$; $P < 0.001$], which reflected the greater number of high confidence old judgments vs. high confidence new judgments.

I conducted a 3 × 2 repeated measures ANOVA to explore the effect of retrospective confidence ratings (low, medium, high) on accuracy for each category of judgment (old, new). As expected, confidence was predictive of accuracy [$F(2, 62) = 229.72$ $P < 0.001$]. However, an interaction between confidence and old-new judgment was observed such that confidence was more predictive of percent correct during old than new judgments [$F(2, 62) = 75.31$ $P < 0.001$]. Low, medium, and high confidence old decisions were accurate 51%, 76%, and 94% of the time, respectively. Accuracy for new responses varied with a smaller range 77%-87%. The proportion

[1] Due to the ceiling effects, the accuracy of high confidence old responses result in less variance than the other conditions in the ANOVA. However, ANOVA is robust to violations in homogeneity of variance, so I opted for this analysis over a more complicated procedure.

of responses for each confidence level also differed between old and new judgments. Less than 30% of old judgments were made with low confidence compared to 40% of new judgments. When taken collectively, the larger number of low confidence new judgments and the near-chance accuracy of low confidence old judgments suggest that lures may be more susceptible to influence of reward contingencies. In other words, reward contingencies are likely more likely to affect false alarm rates than hit rates in this data set.

Similar effects of retrospective confidence were observed for response time (RT). Figure 4B shows that RT followed a classic inverted U-shape distribution with the greatest latencies occurring during low confidence judgments (Murdock and Dufty, 1972; Ratcliff and Murdock, 1976). I conducted a 2 × 3 repeated measures ANOVA to explore the effect of confidence (low, medium, high) on RT during each type of decision (old, new). Subjective confidence was negatively correlated with RT [$F(2, 62) = 92.11$, $P < 0.001$]. In addition, commitments to old decisions were made more quickly than new decisions [$F(1, 31) = 40.13$, $P < 0.001$]. Further, I observed an interaction between confidence and decision type such that the effect of confidence on RT was greater for old than new judgments [$F(2, 62) = 33.11$ $P < 0.001$]. Mean median RT for high confidence old judgments was nearly a half second faster than low confidence old decisions (1,222 vs. 1,683 ms).

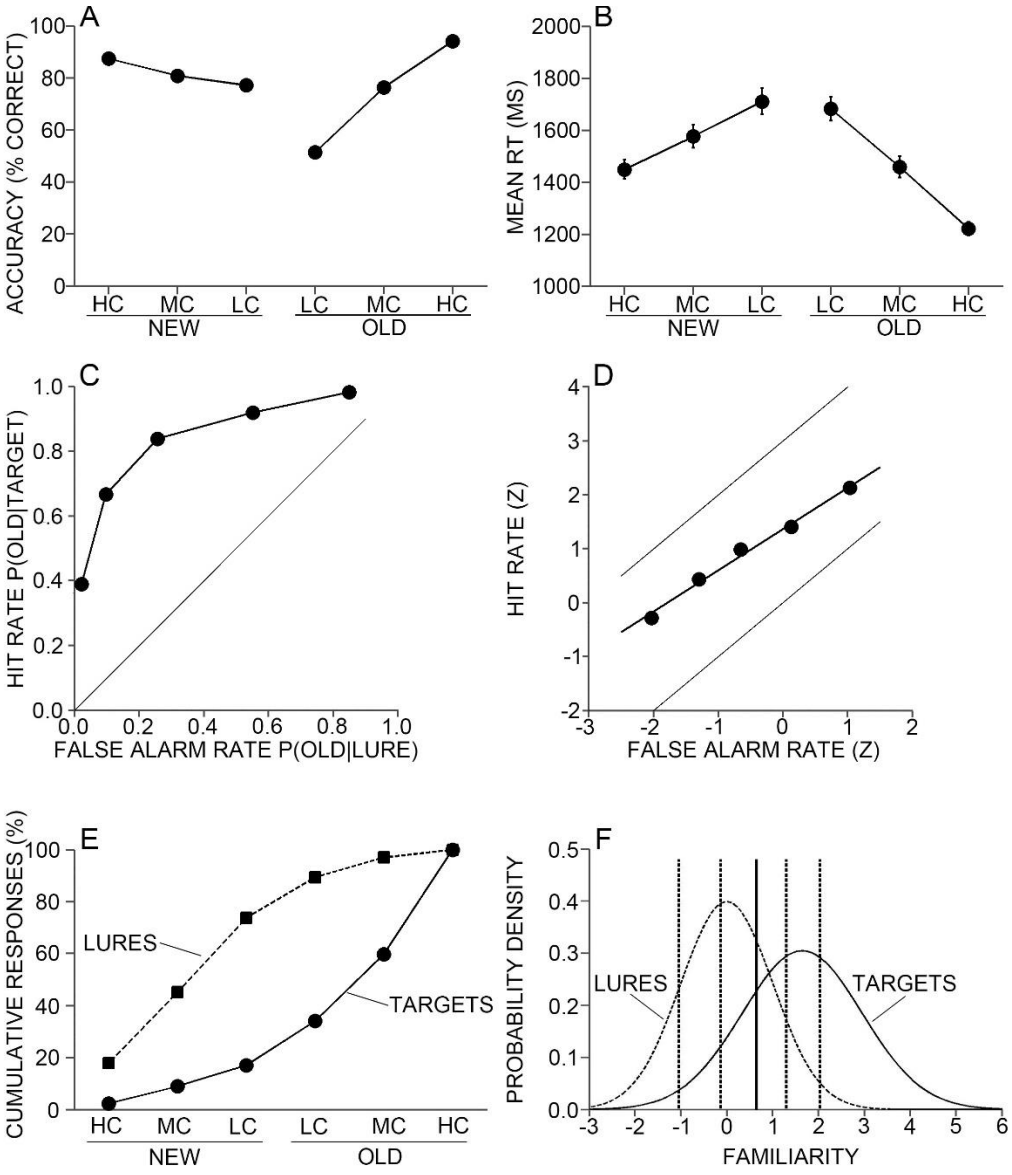


Figure 4. Behavioral results after collapsing across reward contingencies. A) Accuracy (percent correct) as a function of old-new judgment and decision confidence including low (LC), medium (MC), and high confidence (HC) responses. **B)** Mean median response time as a function of old-new judgment and decision confidence. **C)** Receiver operating characteristic (ROC) curve for all recognition data. **D)** Z-transformed ROC curve. Black diagonal lines represent slopes of 1. **E)** Mean empirical cumulative distribution function displaying the frequency of each response choice for both targets and lures. **F)** Estimation of the unequal signal detection model target distributions. The relative variance of the signal distribution is computed based on the slope of the Z-ROC curve in **D**. The old-new criterion is shown as a solid horizontal black line. The criteria associated with each level of confidence are shown as dotted horizontal black lines.

Interactions between Choice and Reward Contingency

Figure 5 shows group-averaged frequency, accuracy, and median response times as a function of item history (target, lure) and reward contingency (CR-I, L-R, H-R, and Hit-I). A 2 × 4 repeated measures ANOVA revealed significant differences in the number old and new judgments subjects made in each reward contingency condition. As reported above, old judgments were generally made more frequently than new judgments leading to a liberal response bias in favor of old responses [$F(1, 31) = 19.30$, $P < 0.001$]. However, there was a significant interaction between reward contingency and the ratio of old to new judgments [$F(3, 93) = 14.90$, $P < 0.001$]. Subjects made more old than new judgments in both of the neutral reward contingency conditions (L-R and H-R) as well as the Hit-I condition [paired t test; all $P < 0.001$]. However, the numbers of old and new judgments made by subjects were statistically equivalent in the CR-I condition [$t(31) = 1.20$, $P = 0.238$].

Table 4. Mean Signal Detection Statistics as a Function of Reward Contingency

Reward Condition	Hit Rate	FA Rate	d’	C	Hit RT	CR RT
CR-Incentive (CR-I)	0.78 (0.68)	0.18 (0.37)	1.72	0.07	1456 (208)	1577 (261)
Low-Reward (L-R)	0.86 (0.63)	0.25 (0.50)	1.75	-0.21	1293 (176)	1534 (249)
High-Reward (H-R)	0.86 (0.62)	0.26 (0.44)	1.74	-0.22	1305 (211)	1540 (252)
Hit-Incentive (Hit-I)	0.86 (0.67)	0.33 (0.67)	1.53	-0.32	1329 (219)	1577 (216)

Standard deviations are in parentheses.

Average hit and false alarm rates as a function of reward contingency are provided in Table 4. Hit and false alarm rates were entered into a repeated measures ANOVA with factors of

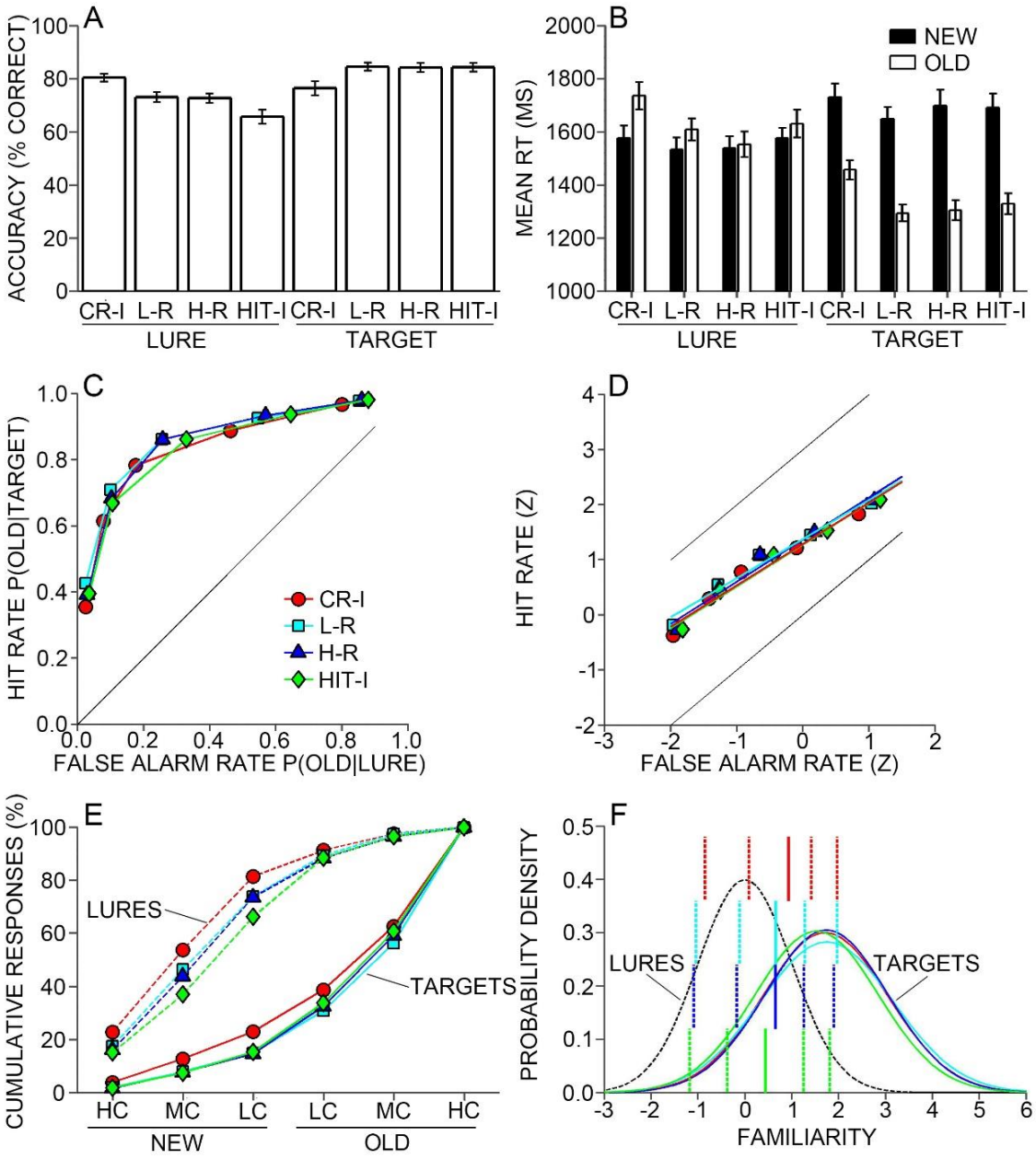
reward contingency and item history (for targets: hit rate; for lures: false alarm rate). The probability that a participant made an old response to a presented item was significantly influenced by item history [$F(1, 31) = 1097.21$, $P < 0.001$] as well as the reward contingency [$F(3, 93) = 15.21$, $P < 0.001$]. Close inspection of the effect of reward contingency on participant responses reveals the greatest effect of reward contingency was on false alarms (Figure 5A). Participants accurately classified 74% of the lures as new in the conditions with neutral reward contingencies (L-R and H-R). Accuracy in classifying lures dropped to 66% correct in the Hit-I condition and rose to 80% correct in the CR-I condition. In contrast, participants accurately classified 85% of the targets as old in all conditions except for the CR-I condition, where performance dropped to 77% correct. The significance of this observation was confirmed by ANOVA; the effect of reward contingency on the probability of an old response interacted with item history such that reward contingency had a greater effect on the categorization of lures than targets [$F(3, 93) = 4.50$, $P = 0.005$].

The preceding accuracy results predict that the largest impact of choice bias on brain activity will be found by examining lure trials (i.e. false alarms vs. correct rejection trials). Since there can be no increase in the familiarity of the lures in the Hit-Incentive condition, any difference between false alarms and correct rejections as a function of reward contingency reflects a difference in choice bias.

Discriminability (d') and choice bias (C) were computed for each participant and averaged (Table 4). Discriminability was similar across reward contingencies [$F(3, 93) = 2.42$, $P = 0.071$], and the estimated signal detection gaussians were nearly identical in each reward contingency (Figure 5F). In contrast, choice bias was robustly modulated by cue condition [$F(3, 93) = 12.50$, $P < 0.001$]; C was much lower for the Hit-I than CR-I condition [C(Hit-I) = -0.32;

C(CR-I) = 0.07]. These results demonstrate that the manipulation of reward contingencies had the predicted effect on accuracy, namely a shift in response criterion consistent with the reward manipulation.

Figure 5B shows median response time averaged across participants for each old or new judgment as a function of item history and reward contingency (see also Table 4). Data were entered into a repeated measures ANOVA with factors of reward contingency (CR-I, L-R, H-R, and Hit-I) and accurate old-new judgment (Hit, CR). Median response times were significantly influenced by reward contingency [$F(3, 93) = 10.06$, $P < 0.001$]; asymmetric reward contingencies led to slower RTs. In addition, a robust main effect of correct old-new judgment was observed [$F(1, 31) = 66.83$, $P < 0.001$]; CRs were slower than hits. In addition, there was a significant interaction between reward contingency and target-lure status [$F(3, 93) = 7.22$, $P < 0.001$]. The interaction reflected the fact that although correct responses were faster to targets than lures, the difference was greater during the Hit-I than the CR-I condition.


A
ACCURACY (% CORRECT)
100
80
60
40
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CR-I L-R H-R HIT-I CR-I L-R H-R HIT-I
LURE
TARGET
B
MEAN RT (MS)
2000
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OLD
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-3 -2 -1 0 1 2 3 4 5 6
FAMILIARITY

Figure 5

Figure 5 (Continued). Behavioral results after collapsing across reward contingencies **A)** Accuracy (percent correct) as a function of item history (target or lure) and reward contingency including correct rejection-incentive (CR-I), low reward (L-R), high reward (H-R), or hit-incentive (HIT-I) conditions. **B)** Mean median response time as a function of item history, and reward contingency are presented for both old and new judgments. **C)** Receiver operating characteristic (ROC) curve as a function of reward contingency. The relative position of the decision criterion for each response type determines the location of the points on the curve. Notice that the data points are generally shifted to the left in the CR-I condition and to the right in the HIT-I condition relative to the neutral reward contingency conditions L-R and H-R. Although asymmetric reward contingencies induced criterion shifts that altered the position of the points on the curve, the basic shape of the curve remained constant. **D)** Z-transformed ROC curve. Black diagonal lines represent slopes of 1. **E)** Mean empirical cumulative distribution function displaying the difference between the CR-I, L-R, H-R, and Hit-I reward conditions for both lures and targets. Note that the reward contingency had a greater effect on confidence ratings to lures than targets. **F)** Estimation of the unequal signal detection model target distributions for each reward contingency. The relative variance of the signal distribution is computed based on the slope of the Z-ROC curves in **D**. The old-new criteria are shown as solid horizontal lines. The criteria associated with each level of confidence are shown as dotted horizontal lines.

Resting State fMRI Functional Correlation Results

Before exploring the effects of subjective judgments and reward contingencies on brain activation, I estimated the anatomical location of the two prominent brain networks that are commonly engaged during recognition memory tasks, which include the frontoparietal and hippocampal-cortical networks. To generate estimates the intrinsic functional anatomy of these networks, I correlated the time course of spontaneous BOLD fluctuations measured within *a priori* defined seed regions and the time course of activity in each voxel of the brain. Voxels correlated with each of the seed regions are shown projected onto the inflated cortical surface in Figure 6. The network of regions correlated with spontaneous fluctuations in the pPHG or vpIPL were highly similar and included ventral medial prefrontal, superior prefrontal, lateral temporal, posterior parietal, and retrosplenial extending into posterior cingulate and parietal cortices (Figure 6, A and B). The network of regions correlated with spontaneous fluctuations aPFC and alIPS were also very similar and included an extensive swath of lateral prefrontal, dorsal medial prefrontal, lateral temporal, intraparietal sulcus extending into supramarginal gyrus (Figure 6, C and D). Each of the *a priori* ROI shown in blue was carried forward for analyses of task-evoked activation (see Table 3).

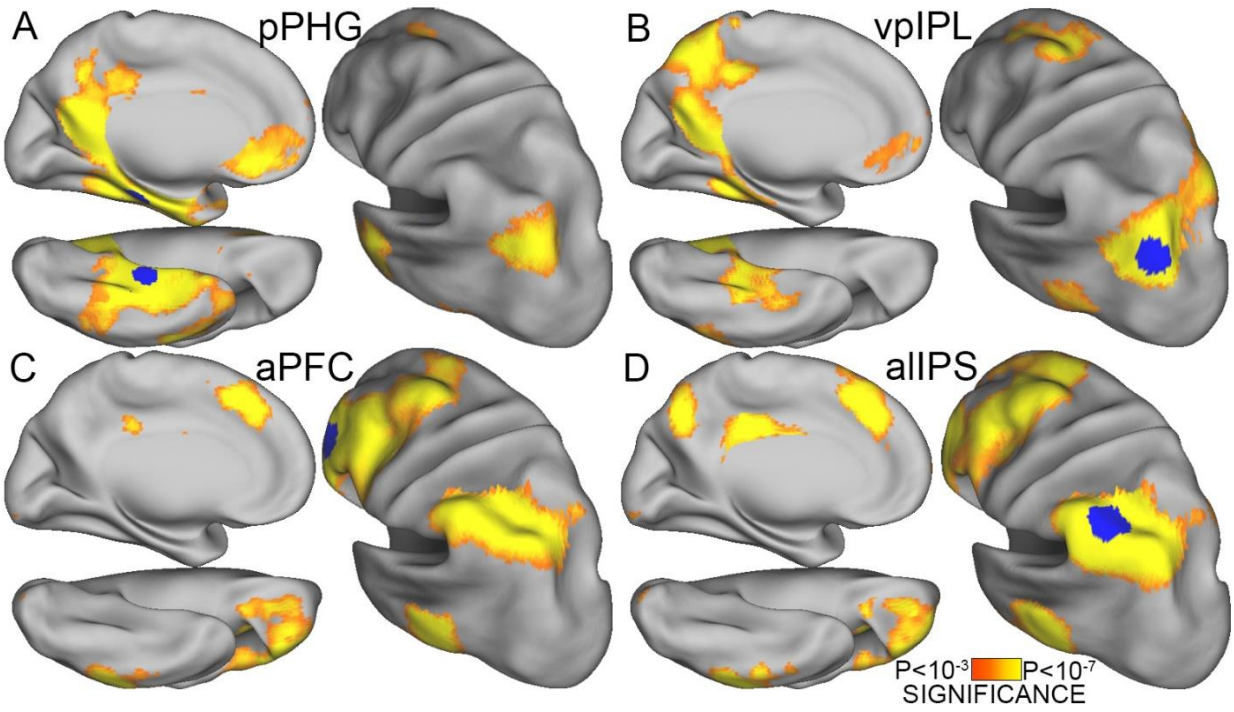

Figure 6. Resting state functional connectivity maps. Spontaneous BOLD correlations in 32 humans associated with seed regions in **A)** pPHG **B)** vpIPL **C)** aPFC and **D)** alIPS. Seed regions are shown in blue and on the right side of Figure 3.

Task Activation fMRI Results

Familiarity

Retrieval success is the phenomenological experience of accompanying accurate memory for the past and is determined by the participant's ability to discriminate targets from lures. Previous studies have operationalized retrieval success as the difference in brain activation between hits and CRs. Interest in the role of parietal cortex in episodic memory was initially trigged by consistent engagement of parietal cortex during retrieval success. To relate the present results to prior studies, I began by contrasting hits and CRs. All four *a priori* ROIs were significantly more activated by hits than CRs, including pPHG [$t(31) = 3.89$ $P < 0.001$), vpIPL ($t(31) = 4.89$ $P < 0.001$), aPFC ($t(31) = 3.32$ $P = 0.002$), and alIPS ($t(31) = 5.18$ $P < 0.001$].

These results demonstrate that the neural correlates of retrieval success include regions from within both the hippocampal-cortical network and the frontoparietal network.

To understand the roles of these two networks in memory retrieval, it will be informative to examine how these regions respond during error trials. Retrieval theory and dual-process theory have different predictions about the response of parietal cortex during false alarms. According to retrieval theory, a decision variable integrates all sources of evidence, priors, and value to plan a decision (and usually a motor response). A decision variable always correlates with the eventual decision and would therefore be activated by false alarms as well as hits. In contrast, dual-process theory would predict that a parietal region that supports recollection would not be engaged during false alarms, which are associated with low confidence, made on the basis of familiarity, and unlikely to be accompanied by recollected content.

Figure 7 shows activation levels in *a priori* ROIs during old or new judgments to targets and lures. A 2×2 ANOVA consisting of item history (target, lure) x decision category (old, new) was conducted for aPFC, alIPS, pPHG, and vpIPL. Strong main effects of decision category were found in both pPHG [$F(1, 31) = 19.58$, $P < 0.001$] and vpIPL [$F(1, 31) = 25.99$, $P < 0.001$]. Activation in both regions of the hippocampal-cortical network was strongly correlated with the subjective perception that an item is old regardless of accuracy. Hypothesis-driven tests demonstrated that the hippocampal-cortical system is activated by the false perception of familiarity. Both the pPHG and the vpIPL were significantly activated by false alarms when compared to correct rejections (pPHG: ($t(31) = 3.16$, $P = 0.004$; vpIPL: ($t(31) = 4.79$, $P < 0.001$). In both the pPHG and vpIPL, the magnitude of activation for hits and false alarms was statistically identical (Ps ≥ 0.239). In the present data set, vpIPL activation was observed during both hits and false alarms. This pattern of activation is consistent with a role as a decision

variable as posited by retrieval theory. Robust vpIPL activation during false alarms is inconsistent with an exclusive role in recollection, which would be posited by a dual-process theory account of parietal cortex.

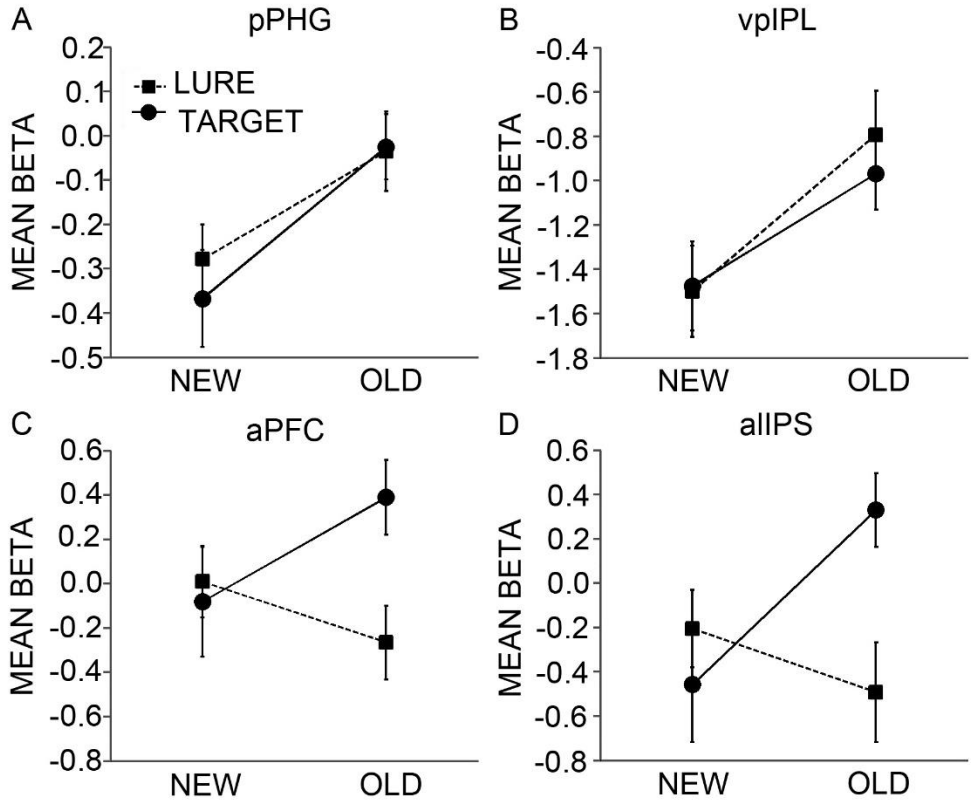

Figure 7. Parahippocampal gyrus and posterior parietal cortex are activated by the perception that an item is old. Mean and standard errors of the parameters estimates extracted from *a priori* regions of interest defined in and around **A)** pPHG, **B)** vpIPL, **C)** aPFC, and **D)** alIPS.

In contrast, a robust interaction between item history and categorical decision was observed in both aPFC [$F(1, 31) = 8.57$, $P = 0.006$] and alIPS [$F(1, 31) = 15.35$, $P < 0.001$]. A significant main effect of item history was also observed in alIPS [$F(1, 31) = 5.34$, $P = 0.028$]. In the contrast to the pattern observed in the hippocampal-cortical network, the regions of the frontoparietal network were not activated during false alarms. In fact, activation in both aPFC

and alIPS was marginally reduced during false alarms compared to correct rejections (aPFC: $t(31) = -2.39$, $P = 0.023$; alIPS: $t(31) = -1.79$, $P = 0.083$). In the present data set, activity in the frontoparietal network, including the alIPS, is incompatible with a role as a mnemonic decision variable (or mnemonic accumulator) as specified by retrieval theory because activation in this network is note greater during false alarms than correct rejections.

Examination of false alarm trials suggests functional heterogeneity in parietal responses during recognition memory. This hypothesis was confirmed with ANOVA. A 2 × 2 ANOVA with factors of parietal region (alIPS, vpIPL) and judgment to presented lures (FA, CR) revealed a significant interaction [$F(1, 31) = 19.25$, $P < 0.001$].

Figure 8 shows an exploratory, whole-brain contrast of retrieval success (hits vs CRs) and false alarm effects (FAs vs CRs). Consistent with previous reports, retrieval success was associated with significant activation in parahippocampal, anterior prefrontal, dorsolateral prefrontal, ventromedial prefrontal, lateral temporal, posterior inferior parietal, intraparietal sulcus, and posterior medial cortex extending from retrosplenial into posterior cingulate and precuneus cortex. Comparison of Figure 6 and 8 demonstrates that both the frontoparietal and hippocampal-cortical networks are engaged during retrieval success. In contrast, false alarms were associated with activation in posterior parahippocampal, ventral posterior parietal, retrosplenial, and posterior cingulate cortex. The false alarm map is a subset of the retrieval success map and appears to contain the core components of the hippocampal-cortical network shown in Figure 6.

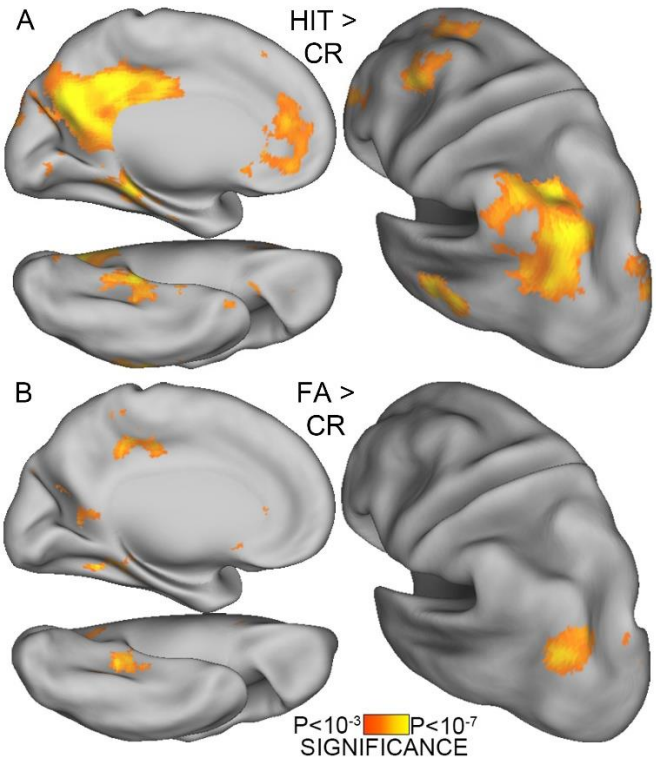

Figure 8. Whole-brain activation maps reveal dissociation between retrieval success and false memory. A) Statistical activation maps for BOLD signal increases between hit and correct rejection (CR) trials. **B)** Statistical activation maps for BOLD signal increases between false alarm (FA) and correct rejection (CR) trials. Both contrasts are thresholded at $P < 0.001$ (uncorrected).

In this data sample, participants were nearly twice as likely to make high confidence old than high confidence new judgments. On average, high confidence decisions comprised 40% of old judgments and 22% of new judgments. This disparity in retrospective confidence ratings between old and new judgments is similar to previous studies (e.g. Daselaar et al., 2006) and suggests that the retrieval success contrast may be confounded by large differences in subjective confidence between old and new judgments. To reduce the impact of this confound on the analyses, I attempted to control subjective confidence by directly comparing medium confidence hits to medium confidence CRs. The vpIPL was significantly more activated by medium confidence hits than medium confidence CRs [$t(31) = 2.80$, $P = 0.009$). To the extent that medium confidence ratings for old and new judgments were equivalent, this result demonstrates that the retrieval success effect in vpIPL is not driven solely by subjective confidence. In

contrast, none of the other 3 *a priori* ROIs showed retrieval success effects when only medium confidence decisions were included in the analyses (all P's > 0.173).

To further understand the roles of these two networks during recognition memory, I examined the effect of retrospective confidence ratings on activation. Retrieval theory and dual process theory have similar predictions about the response of parietal cortex as a function of confidence rating. According to retrieval theory, a decision variable will correlate with the strength of the evidence in favor of an old judgment. Therefore, parietal cortex should be least activated during high confidence new decisions and most activated by high confidence old trials. Dual-process theory makes similar predications about a region that is sensitive to the process of familiarity. In contrast, dual-process theory predicts that a region selective to recollection will only be activated during high confident old judgments. Brain regions that support the process of recollection are not expected differ between low confidence old judgments and new judgments.

Figure 9 shows task-related activation within each *a priori* ROI during either old or new judgments as a function of retrospective confidence rating. Activation in the pPHG was greater during high confidence old judgments than either low confidence old judgments [$t(31) = 4.03$, $P < 0.001$] or high confidence new judgments [$t(28) = 3.58$, $P = 0.001$]. Critically, high confidence new judgments were not greater than low confidence new judgments [$t(28) = 0.85$, $P = 0.402$]. These results a consistent with the hypothesis that activation in pPHG correlates with familiarity. Similarly, activation in the vpIPL was greater during high confidence old judgments than either low confidence old judgments [$t(31) = 2.81$, $P = 0.009$] or high confidence new judgments [$t(28) = 3.93$, $P = 0.001$]. The vpIPL was not more activated by high confidence new judgments than low confidence new judgments [$t(28) = -0.05$, $P = 0.958$]. Once again the vpIPL activation pattern was broadly similar to that of pPHG and correlated with familiarity strength. As

previously outlined, dual process theory predicts that a region responsive to recollection would not be engaged during low confidence old judgments. However, a direct test of this prediction suggested that the response in vpIPL was greater during low confidence old vs. low confidence new judgments [$t(31) = 1.90$, $P = 0.034$, one-tailed]. Although the low confidence old-new effect is weak, it is nevertheless inconsistent with the hypothesis that vpIPL is exclusively activated during recollection judgments.

Further analysis of the relation between retrospective confidence ratings and activation in the frontoparietal network suggested that the interactions observed in Figure 7 were largely driven by differences in subjective confidence between old vs. new judgments. While activation in the aPFC was greater during high confidence old judgments than low confidence old judgments [$t(31) = 3.26$, $P = 0.003$], the response in aPFC was statistically equivalent during high confidence old and new judgments [$t(28) = 1.21$, $P = 0.237$]. Furthermore, the aPFC was more activated by high confidence new judgments than low confidence new judgments [$t(28) = 3.79$, $P = 0.001$]. This result suggests that the aPFC plays a role in the metacognitive aspects of decision making, and is not sensitive to subjective familiarity. Activation in the alIPS was greater during high confidence old judgments than low confidence old judgments [$t(31) = 6.26$, $P < 0.001$] and high confidence new judgments [$t(28) = 3.08$, $P = 0.005$]. These results suggest that, unlike aPFC, the alIPS may have access to internal familiarity signals. However, alIPS activation during high confidence new judgments was marginally greater than low confidence new judgments [$t(28) = 2.01$, $P = 0.054$]. The fact that high confidence new judgments evoked more activation in alIPS than low confidence new judgments is inconsistent with a role as a mnemonic decision variable or an exclusive role in recollection. Further, the generic effect of retrospective confidence on brain activation in both aPFC and alIPS is consistent with the

interpretation that retrieval success effects in the frontoparietal network are at least partially explained by factors indirectly related to memory retrieval, such as retrospective evaluation of confidence.

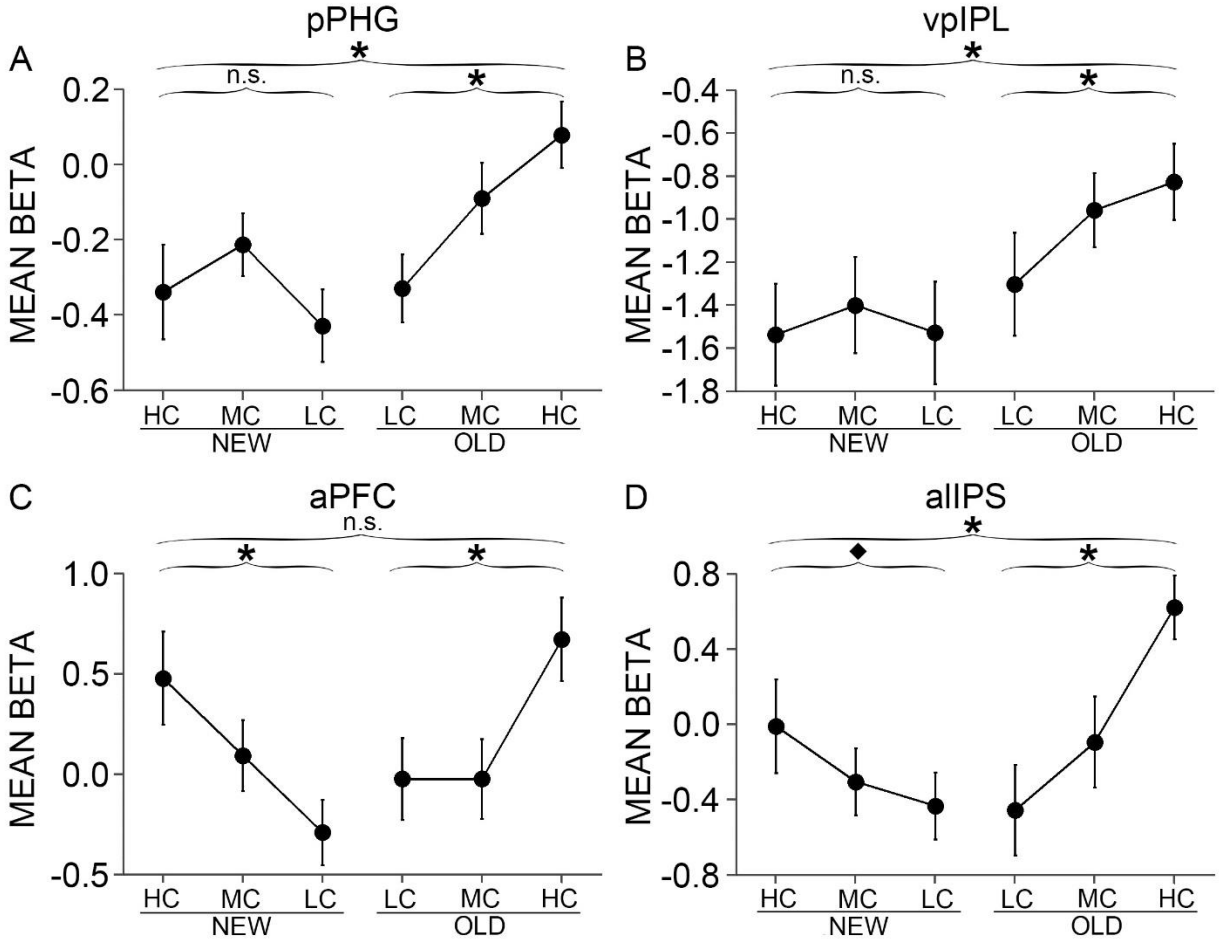

Figure 9. Activation in the hippocampal-cortical network is correlated with confidence that an item is old while activation in frontoparietal network is associated with high confidence for both old and new judgments. Mean and standard errors of the parameters estimates extracted from *a priori* regions of interest defined in and around **A)** pPHG, **B)** vpIPL, **C)** aPFC, and **D)** alIPS. Significant comparisons are indicated with stars. One comparison was marginally significant ($P = 0.054$) and is indicated with a diamond. n.s. = not significant.

Context

Recognition memory decisions depend on the interaction of mnemonic processes and control processes that set goals and expectations for performance. Therefore, to fully understand the roles of these two brain networks during memory retrieval, it will be informative to examine how these regions respond during contextual cues that induce shifts in decision criterion. The next set of analyses address the impact of reward contingencies on brain activation. Contrasts between conditions will be used to further evaluate major theories of parietal function during memory retrieval.

Each major theory of parietal function has hypotheses about how parietal cortex will respond to biasing cues. Dual-process theory predicts that a region selectively engaged by recollection would not be modulated by reward cues; a region that is modulated by biasing cues would not solely reflect a recollection signal, but also the 'target value' of the stimulus. Retrieval theory predicts that a decision variable will respond differentially to reward cues because the decision variable represents both evidence and choice bias. Specifically, cues that increase the target value of the item (H-R or Hit-I) or induce a liberal criterion (Hit-I) would increase activation whereas cues that lower the target value (L-R or CR-I) or induce a conservative criterion (CR-I) would result in reduced activation. In contrast, a mnemonic accumulator would be predicted to show the opposite profile of a decision variable in response to cues that induced choice bias. A mnemonic accumulator represents the quantity of evidence in favor of a decision; more evidence would be required under a strict criterion. For example, more accumulation of familiarity evidence would be required on CR-I relative to Hit-I trials because the criterion is more distant on CR-I trials. The AtoM theory posits that dorsal parietal cortex (but not ventral parietal cortex) maintains retrieval goals to guide top-down attention to memory

retrieval processes. Asymmetric reward conditions that incentivized hits or correct rejections require greater top-down control than symmetric reward conditions that set an equal value for each choice. Therefore, AtoM would expect dorsal (but not ventral) parietal cortex to be more engaged during asymmetric than symmetric incentive trials. The AtoM and mnemonic accumulator hypotheses have the same prediction about the effect of reward contingency in ventral parietal cortex.

A 2 × 2 ANOVA consisting of target reward value (high, low) and target-lure reward contingency symmetry (asymmetric, symmetric) was conducted for aPFC, alIPS, pPHG, and vpIPL. The alIPS showed a main effect of reward contingency symmetry [$F(1, 31) = 5.34$; $P = 0.028$]. Consistent with the predictions of AtoM, the alIPS was more activated on trials when the reward contingency was asymmetric than trials when the reward contingency was symmetric. No main effect of reward or interaction between reward and symmetry were observed in alIPS. No significant effects were observed in aPFC. The greater engagement of alIPS during asymmetric reward conditions was consistent with slower response times on asymmetric reward trials and may reflect then need for greater levels of cognitive control as predicted by AtoM theory. No significant effects of reward or symmetry were observed in vpIPL. However, a robust effect of target reward was observed in pPHG [$F(1, 31) = 11.25$, $P = 0.002$]. This effect reflected the fact that pPHG was more engaged on trials where targets were associated with a high vs. low reward (H-R and Hit-I conditions). No other effects were observed in pPHG.

Most of the present research is motivated by the observation that regions within both the hippocampal-cortical and frontoparietal networks are engaged during retrieval success (hits vs. CRs). To determine whether the retrieval success effect is influenced by the reward contingencies, I conducted a 4 × 2 ANOVA to detect any effect of reward contingency (CR-I, L-

R, H-R, Hit-I) on the retrieval success effect (hits, CRs). Consistent with the results described above, a main effect of retrieval success was observed in all four *a priori* ROIs (all *P*s ≤ 0.007). However, the retrieval success effect did not interact with reward contingency in any of the ROIs (all *P*'s ≥ 0.377). A main effect of reward contingency was observed in pPHG [$F(3, 93) = 2.90$, $P = 0.039$].

The earlier analyses established a strong relationship between the ventral posterior inferior parietal lobule and subjective familiarity. In contrast, the intraparietal sulcus was more associated with aspects of decision making, such as retrospective confidence and the symmetry of reward contingencies. In the present study, the most salient functional difference between the two parietal regions was found in the response during false alarm trials relative to correct rejection trials (Figure 7). False alarms can emerge from at least two sources. A false sense of familiarity emerging from misleading mnemonic representations may trigger old judgments to lures. Another source of false alarms would be top-down biasing signals that favor old or new responses in the presence of decision uncertainty. As detailed in the behavioral results, the reward contingency manipulation had the greatest effect on the number of false alarm errors during the presentation of lures. Therefore, I asked if the reward contingency also had an effect on activation in parietal cortex during false alarms relative to correct rejections.

To determine whether the false alarm effect is influenced by the reward contingencies, I conducted a 4 × 2 ANOVA to detect any effect of reward contingency (CR-I, L-R, H-R, Hit-I) on the old-new decision to presented lures (FAs, CRs). Each of the four *a priori* ROIs showed a main effect of old-new decision. Increased activation was found for FAs relative to CRs in both the pPHG [$F(1, 29) = 14.72$, $P = 0.001$] and the vpIPL [$F(1, 29) = 20.53$, $P < 0.001$]. Decreased activation was found for FAs relative to CRs in both the aPFC [$F(1, 29) = 4.77$, $P = 0.037$] and

the alIPS [$F(1, 29) = 4.64$, $P = 0.040$]. A main effect of reward contingency was only found in pPHG [$F(3, 87) = 3.40$, $P = 0.021$], but none of the other ROIs. No interaction between reward contingency and old-new decision was found in any of the *a priori* ROIs.

There was no interaction between reward contingency and retrieval success (i.e. Hits vs. CRs) or old vs. new responses to lures (i.e. FAs vs. CRs) in any of the ROIs interrogated in this study, including those in parietal cortex. However, there remains the possibility that there may be an interaction between dorsal and ventral parietal cortex such that greater activation in ventral parietal cortex is required for an old decision in the presence of an induced conservative response criterion represented by dorsal parietal cortex. If dorsal parietal cortex functions to adaptively bias old decisions as predicted by AtoM theory, then one would predict that cues that induced a liberal decision criterion would increase false alarm activation whereas cues that induced a conservative criterion would result in reduced false alarm activation. The AtoM theory also posits that the role of ventral parietal cortex is to monitor internal mnemonic information and act as a circuit breaker to signal the need to direct attention to the retrieval of relevant memories. If the circuit breaker hypothesis is correct, then ventral parietal cortex will be more engaged during false alarms occurring in the context of a conservative criterion relative to a liberal decision criterion because the evoked familiarity of the stimulus must be sufficient to override the choice bias and direct attention to the retrieved information.

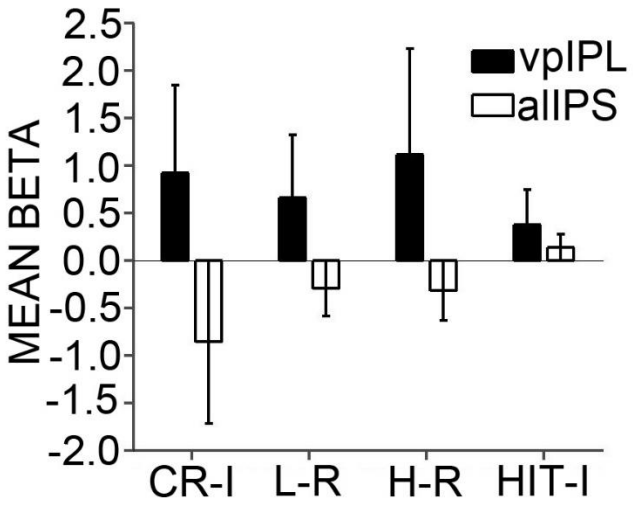

Figure 10. Regional interaction between vpIPL and alIPS as a function of reward contingency (CR-I, L-R, H-R, Hit-I) and response to presented lures (FA, CR). Mean and standard errors of the parameters estimates extracted from *a priori* regions of interest defined in and around vpIPL and alIPS.

Figure 10 shows the false alarm effect for each parietal region as a function of reward contingency. Earlier, I reported a significant interaction between parietal region (alIPS, vpIPL) and judgment to presented lures (FA, CR); the false alarm effect was robust in vpIPL and absent in alIPS. Here, I asked if this relationship interacted with reward contingency. A three-way ANOVA employing factors of region (alIPS, vpIPL), judgment to presented lures (FA, CR), and reward contingency (CR-I, L-R, H-R, Hit-I) revealed a significant three-way interaction [$F(3, 87) = 4.25$, $P = 0.008$]. This effect emerged because the vpIPL was more activated and the alIPS was more deactivated by false alarms in the CR-I relative to the Hit-I condition. To clearly resolve the source of the interaction, I separately conducted a 2 × 4 ANOVA with region and reward contingency for each response type (FA, CR). The interaction between region and reward contingency was not significant on correct rejection trials [$F(3, 93) = 2.03$, $P = 0.115$]. However, there was a significant interaction between region and reward contingency on false alarm trials [$F(3, 87) = 3.54$, $P = 0.018$]. This interaction suggests that the two parietal regions may respond differentially to factors influencing choice bias when making false alarms. As

predicted by the AtoM theory, vpIPL was numerically higher and alIPS was numerically lower on the CR-I compared to the Hit-I false alarm trials.

Discussion

The present experiment tested existing theories of parietal contributions to memory by examining the relation between behavioral choices and brain activity during an old-new recognition memory task with reward contingencies. Three discoveries are reported regarding the location and function of regions in the brain that underlie memory decisions. First, retrieval success prominently engages two large-scale brain networks, the hippocampal-cortical network and the frontoparietal network (Figures 6, 7, and 8). Second, the activation within each of these two networks was correlated with distinct cognitive representations (Figures 7, 9, and 10). The hippocampal-cortical network was most activated during old decisions (Figure 7), was engaged during both hits and false alarms (Figure 7), and was activated during low confidence old vs. low confidence new judgments (Figure 9). In contrast, while the frontoparietal network was robustly activated by hits (Figure 7), it was not activated during false alarms (Figure 7) or low confidence old judgments (Figure 9). Furthermore, unlike regions the hippocampal-cortical network, regions within the frontoparietal network were more activated during high vs. low confidence new responses (Figure 9), which suggests this network plays a more generic role in decision making. Third, choice bias manipulations may have opposing effects on false alarm activation in the parietal components of these two networks (Figure 10). These observations suggest a dual network model of recognition memory decision making and constrain current theories of the role of parietal cortex in episodic memory.

Parietal Cortex and Mnemonic Strength

Neuroimaging data suggest that parietal cortex represents information associated with the strength of the memory or the recollection of episodic details. Mnemonic strength signals that are

associated with the successful discrimination of old and new items have been consistently found in posterior parietal cortex (Wagner et al., 2005; Ciaramelli et al., 2008; Cabeza et al., 2008; Vilberg and Rugg, 2008). Specifically, greater activation in these regions is consistently observed with fMRI when participants correctly recognize studied targets versus correctly rejected lures. Retrieval success effects are consistently found in parietal cortex regardless of format of mnemonic representation (lexical, acoustic, or pictorial) or the response contingency (Henson et al., 1999; Kahn et al., 2004; Konishi et al., 2000; Leube et al., 2003; McDermott et al., 2000; Shannon and Buckner, 2004; Wheeler and Buckner, 2003; 2004). Studies of recognition memory have used a number of paradigms to examine performance and/or brain activity at multiple levels of memory strength or familiarity either by sorting trials on the basis of depth of encoding (Craik and Lockhart, 1972; Rugg et al., 2000; Shannon and Buckner, 2004) or on the basis of self-reported memory strength via the remember/know procedure (Henson et al., 1999; Wheeler and Buckner, 2004), retrospective confidence ratings (Yonelinas et al., 2005; Montaldi et al., 2006; Daselaar et al., 2006), or source memory (Wilding and Rugg, 1996; Dobbins et al., 2003). Activation in posterior parietal cortex is consistently greater during strong than weak memories, especially when those strong memories elicit the recollection of contextual information (Eldridge et al., 2000; Henson et al., 1999; Wheeler and Buckner, 2004; Yonelinas et al., 2005; Daselaar et al., 2006; Montaldi et al., 2006; Vilberg and Rugg, 2007). Moreover, the left ventral posterior parietal cortex is sensitive to the quantitative amount of recollected pictorial (Vilberg and Rugg, 2007; Guerin and Miller, 2011) and verbal material (Vilberg and Rugg, 2009b).

Although electroencephalography to has limited spatial resolution, several studies have demonstrated retrieval success effects in electrodes placed over parietal cortex. A probable

neural correlate of the parietal/posterior limbic retrieval success effect is observed as positive posterior ERP activity between 500 and 800 ms post-stimulus, which is often referred to as the parietal old-new effect (Neville et al., 1986; Rugg and Nagy, 1989; Donaldson and Rugg, 1998; Rugg et al., 1998; Rugg and Wilding, 2000). The parietal old-new effect is greatest during recognition decisions associated with recollection, including successful source judgments (Wilding and Rugg, 1996; Senkfor and Van Petten, 1998; Curran, 2004; Düzel et al., 1997; Smith, 1993).

Behavioral research suggests that regions that represent mnemonic strength would be invariant to manipulations that affect choice bias, such as priors or value asymmetries (Snodgrass and Corwin, 1988). Accordingly, posterior lateral parietal cortex (in or around the angular gyrus) is more active for hits than correct rejections, but not significantly influenced by manipulations of the joint probability of old and new items in a recognition test. (Herron et al., 2004; Vilberg and Rugg, 2009a). Further, the parietal positive ERP between 500 and 800 ms post-stimulus is greater for hits than correct rejections independent of joint old:new probability (Friedman, 1990; Smith and Guster, 1993; Herron et al., 2003). Similarly, in a study of asymmetric old:new reward contingencies, the parietal response between 500 and 800 ms was more active for old than new items for both liberal and conservative conditions, but not reliably modulated by choice bias (Curran et al., 2007). The present results also failed to find a significant effect of reward contingencies on activation in parietal cortex. Taken collectively, these results suggest that posterior parietal cortex contains a region that is strongly correlated with subjective familiarity, but not significantly influenced by manipulations of choice bias.

While electrophysiology and functional imaging strongly suggest a role for parietal cortex in episodic memory, it is unclear that parietal cortex is necessary for memory retrieval

(Wagner et al., 2005). Lesions in parietal cortex are generally associated with deficits in spatial attention (Mesulam, 1999) or motor planning (Heilman and Gonzalez Rothi, 1993). However, some recent studies suggest that subtle memory deficits may result from lesions to the posterior parietal lobe (Berryhill et al., 2007; Davidson et al., 2008; Simons et al., 2010; Ciaramelli et al., 2010). For example, two patients with extensive bilateral parietal damage were able to successfully recall autobiographical memories, but the memories lacked contextual details (Berryhill et al., 2007). These same patients also have reduced confidence in source recollection judgments (Simons et al., 2010). Despite the results of these studies, several other reports suggest that parietal damage does not significantly impair recognition memory (Simons et al., 2008; Haramati et al., 2008).

The present study examined correlations between subjective memory strength and brain activation in parietal cortex. Consistent with previous functional imaging studies, I found robust activation in parietal cortex during hits vs. correction rejections. However, the ventral posterior angular gyrus was the only region of parietal cortex that was consistently correlated with subjective familiarity. The vpIPL was more activated during both hits and false alarms. In addition, the vpIPL was more activated during high vs. low confidence old responses. The alIPS was also more activated during hits as well as high vs. low confidence old judgments. However, this region was activated by high vs. low confidence new judgments and not engaged during false alarms, which makes it unlikely that this region of parietal cortex is solely engaged in mnemonic processes.

Many of the studies reviewed above have suggested that the vpIPL plays a direct role in recollection (e.g. Wagner et al., 2005; Vilberg and Rugg, 2008). While the vpIPL may be engaged during recollection, our results suggest that recollection is not necessary for activation

in this region. The vpIPL was activated by low confidence old responses as well as false alarms, which are unlikely to be accompanied by recollected material. Because activation in vpIPL appeared to track subjective familiarity, the present results in vpIPL are more compatible with the mnemonic accumulator or AtoM theory of ventral parietal function.

Parietal Cortex and Choice Bias

Cognitive control processes exert top-down control and guide future behavior according to expectations, priors, value, or intentions (Miller and Cohen, 2001). In recognition memory, cognitive control processes play an essential role in determining the amount of memory strength required before initiating an old judgment. Relevant non-mnemonic information may bias the decision making process and/or adjust the distance between the starting point and the criterial boundary for an old judgment. Both neuroimaging and studies of recognition memory in patients with parietal lesions suggest that parietal cortex may implement adaptive biasing during recognition memory decisions by adjusting the amount of evidence required to initiate an old judgment.

In recognition memory, choice bias and/or brain activity has been experimentally modulated by a number of factors including the manipulation of reward contingencies (Healy and Kubovy, 1978; Curran et al., 2007; Han et al., 2010), participant instructions (Azimian-Faridani and Wilding, 2006), the emotional valence of stimuli (Windmann and Krüger, 1998; Maratos et al., 2000; Windmann and Kutas, 2001), and old:new item probability priors (Healy and Kubovy, 1978; Friedman, 1990; Ratcliff et al., 1992; Wagner et al., 1998; Herron et al., 2003; 2004; Vilberg and Rugg, 2009a). In addition, individual variation in spontaneously

occurring choice bias correlates with individual variation in the magnitude of brain activation at the time of decision making (Windmann et al., 2002; O'Connor et al., 2010).

Asymmetric reward (and punishment) contingencies for hits and correct rejections significantly modulate human behavior (Healy and Kubovy, 1978; Curran et al., 2007) and brain activity (Curran et al., 2007; Han et al., 2010). To examine conflicts between mnemonic strength and choice bias, Curran and colleagues (2007) examined performance and ERP activity during recognition tests with reward value asymmetries that encouraged liberal and conservative decisions. Hit and false alarm rates were greater in the hit-incentive condition relative to the correct rejection-incentive condition. In the brain, early activity in dorsal medial frontal cortex was more negative during false alarms in the correct rejection-incentive condition relative to the hit-incentive condition (Curran et al., 2007). In addition, activity in parietal cortex was more negative for correct rejection-incentive vs. hit-incentive targets (Curran et al., 2007).

Jointly varying the probability of targets and lures in a memory recognition test list can significantly influence choice bias (Ratcliff et al., 1992) and brain activity (Smith and Guster, 1993; Vilberg and Rugg, 2009a; Herron et al., 2003; 2004). In a series of studies manipulating target:lure joint probability, Rugg and colleagues (Herron et al., 2003; 2004; Vilberg and Rugg, 2009a) investigated the influence of the relative probability of target and lure items on ERP and fMRI measured brain activity during recognition judgments. In the Herron studies, the proportion of targets and lures at test was varied across three types of blocks, each containing a low (25%), an equal (50%), or a high (75%) proportion of targets. Probability priors interacted with old-new effects in several regions including anterior prefrontal cortex, posterior inferior frontal cortex, dorsolateral prefrontal cortex, and left lateral parietal cortex (Herron et. al., 2003; Herron et al., 2004; Vilberg and Rugg, 2009a). Low probability items were associated with

sustained baseline activity changes in left prefrontal cortex (Herron et. al., 2003; 2004). In addition, the magnitude of the retrieval success effect in parietal cortex was sensitive to probability priors (Herron et al., 2003; 2004; Vilberg and Rugg, 2009a). O'Connor and colleagues (2010) also demonstrated that activation in parietal cortex was strongly associated with expectations about the old-new status of the upcoming probe using a memory paradigm that is analogous to the Posner cueing task (Posner et al., 1980).

If parietal cortex is sensitive to incentives (Curran et al., 2007) and priors (O'Connor et al., 2010; Vilberg and Rugg, 2009a), then damage to the parietal lobe should result in impairments adjusting the decision criterion during memory judgments. Valid cues or instructions that indicate that there is a low probability of an upcoming target in a recognition memory test list will induce participants to adaptively adopt a conservative decision criterion, which is associated with low false alarm and hit rates (Ratcliff et al., 1992). Recently, Dobbins and colleagues (2012) reported that patients with dorsal parietal lesions have significant impairments adaptively adjusting their decision criterion to incorporate valid informational priors. Specifically, patient false alarm rates were not reduced by cues that validly indicated a high likelihood that the upcoming probe would be a lure. Accordingly, patient hit rates were not reduced by invalid cues that indicated that the upcoming item was likely to be a lure. These studies suggest that parietal cortex may play a role in biasing participants to reject low confidence old judgments.

In the present study we manipulated the reward value of correct old and new decisions in the context of a standard old-new recognition task to examine the effect (if any) on activation in parietal cortex. The asymmetric reward contingencies were successful in shifting participants'

decision criteria and had the greatest effect on the number of false alarm errors (Figure 5). I observed two effects of reward contingency on brain activation in parietal cortex.

First, asymmetric reward contingencies (including both CR-I and Hit-I conditions) resulted in greater activation in the alIPS than symmetric reward contingencies (including L-R and H-R). Greater activation on trials with informative cues could reflect top-down signals that guide decision making, which would be compatible with the AtoM theory of dorsal parietal function. Alternatively, the greater activation observed during asymmetric reward contingencies could reflect the significantly longer responses times recorded on trial types with asymmetric vs. symmetric reward contingencies.

According to AtoM theory, dorsal parietal cortex functions to adaptively bias old decisions according to goals and ventral parietal cortex plays a role in bottom-up attention to internally generated memory (Cabeza et al., 2008). If dorsal parietal cortex functions to represent biases for or against a decision, then the magnitude of parietal activation should be directly correlated with variables that influence goals during recognition decisions, such as reward contingencies. Specifically, one would predict that CR-I cues would reduce activation and Hit-I cues would increase activation in dorsal parietal cortex (similar to Rorie et al., 2010). In other words, the distance between the starting point and the criterion for an old judgment would be decreased following Hit-I cues and increased following CR-I cues. As the decision criterion become more conservative, more activation of ventral parietal cortex is needed to override the choice bias and direct attention to the retrieved information. Accordingly, more familiarity strength and neuronal activation in ventral parietal regions would be required for an old decision on CR-I vs. Hit-I trials. This logic predicts an interaction between biases

represented in dorsal parietal cortex and memory strength signals represented in ventral parietal cortex.

There was a significant interaction between reward contingency and the false alarm effect (FA-CR) across parietal regions (vpIPL, alIPS) (Figure 10). This interaction would be predicted if dorsal parietal cortex represents bias (e.g. Rorie et al., 2010) and ventral parietal cortex represents memory strength. However, despite the significance of this interaction, the effect was too weak to be observed in either of the parietal regions independently. One possibility is that the response bias manipulation was not strong enough to generate robust effects on brain activation. Another possibility is that the effect of response bias on brain activity was invisible due to the blocked design of the study. If the reward contingencies were dynamically altered from trial-to-trial, then an effect of choice bias might be captured in the event-related response. A third possibility is that the effect of reward-induced choice bias was weak because no feedback on accuracy was provided and the reward was provided after the experiment rather than after each correct response. Alternatively, the parietal regions examined in this study may not represent choice bias associated with asymmetric reward contingencies. Future research will be required to determine whether the effect presented in Figure 10 is replicable or can be magnified by trial-by-trial manipulations of response bias.

A Dual-Network Model of Recognition Memory

The process of retrieving episodic memories involves a considerable amount of mental effort, so it should come as no surprise that successful recognition depends on multiple, distributed brain areas (Schacter, 1996). In the case of the old-new recognition memory task, the recognition process may be characterized by at least three distinct processes. First and foremost,

there is the process of remembering. If the probe is recognized, there will be a recovery of the stored memory accompanied with subjective sense of familiarity and perhaps the recollection of components of the original event. Second, there is the decision-making process. Before an old-new judgment can be reached, any retrieved mnemonic content must be evaluated. This process could involve the monitoring of retrieved content, the evaluation of memory strength relative to a decision criterion, or the metacognitive assessment of retrospective confidence. Finally, a motor response must be planned and executed to complete the task.

The task of cognitive neuroscience is to identify the structures that are engaged during successful episodic memory and explain the role these areas play in the retrieval process. Studies in humans, monkeys, and rats have demonstrated that the medial temporal lobe is necessary for the consolidation and retrieval of recently acquired episodic memories (Squire, 1992; Cohen and Eichenbaum, 1993). Neuroimaging (Buckner et al., 1996; Grady et al., 1999) and patient (Pannu and Kaszniak, 2005) studies suggest that multiple areas in the prefrontal cortex may be involved in monitoring and control processes during memory retrieval. Event-related fMRI studies demonstrated that lateral parietal and posterior cingulate cortices are consistently engaged during retrieval and may be associated with memory strength (Wagner et al., 2005; Vilberg and Rugg, 2008; Cabeza et al., 2008). Novel resting state functional connectivity techniques have recently demonstrated that most of the areas engaged during memory recognition are organized into two distinct large-scale brain networks, including a hippocampal-cortical network and a frontoparietal network (Vincent et al., 2006; Vincent et al., 2008; Spreng et al., 2010; O'Connor et al., 2010). Understanding the functions of these two brain networks will be critical for understanding how the brain divides and conquers the challenges of episodic memory retrieval.

The Hippocampal-Cortical Network

The hippocampal formation (including the hippocampus proper, dentate gyrus, subicular complex, posterior entorhinal cortex, and parahippocampal cortex) is critical for the recovery of recently acquired episodic memories (Squire, 1992; Cohen and Eichenbaum, 1993). Surgical or ischemic lesions to the hippocampal formation in humans often leads to temporally graded retrograde amnesia; patients suffer grave loss of recent memories, but remote memories remain relatively intact (Scoville and Milner, 1957; Zola-Morgan et al., 1986). Prospective studies have demonstrated that monkeys with lesions to the hippocampal formation remember remotely acquired memories better than recently acquired memories; moreover, monkeys with lesions in the hippocampal formation perform as well as monkeys without lesions on tests of remote memories (Zola-Morgan and Squire, 1990). The advent of event-related functional neuroimaging permitted memory researchers to observe the patterns of activation in the brain during memory recognition. As expected from lesion studies, hippocampal and parahippocampal cortex are routinely activated during recognition memory (Eldridge, 2000; Wheeler and Buckner, 2004; Daselaar et al., 2006; Vincent et al., 2006).

The hippocampal formation is anatomically and functionally connected with a number of cortical regions that are also engaged during recognition memory. Connections between the hippocampal formation and posterior midline areas, including retrosplenial and posterior cingulate cortices have been documented by several monkey anatomical connectivity studies (Insausti et al. 1987; Kobayashi and Amaral 2003; Lavenex et al. 2002; Suzuki and Amaral 1994; Vogt et al. 1992; Morris et al. 1999; Parvizi et al., 2006) as well as monkey and human functional connectivity studies (Greicius et al., 2004; Vincent et al., 2006; Kahn et al., 2008; Vincent et al., 2007; Vincent et al., 2010; Hutchison and Everling, 2012). In humans, the

hippocampal formation is functionally connected with lateral parietal cortex in or around the posterior inferior parietal lobule (Vincent et al., 2006; Kahn et al., 2008; Figure 6). In monkeys, regions in lateral parietal cortex, including areas 7a and OPT, are anatomically (Blatt et al., 2003; Cavada and Goldman-Rakic, 1989; Kobayashi and Amaral, 2003; Lavenex et al., 2002; Suzuki and Amaral, 1994; Rockland and Van Hoesen 1999; Clower et al. 2001) and functionally (Vincent et al., 2010) connected with the hippocampal formation. Finally, the hippocampal formation of monkeys also has strong anatomical medial prefrontal cortex (Kondo et al., 2005; Lavenex et al., 2002) and lateral temporal cortex (Kondo et al., 2005; Lavenex et al., 2002; Price, 2005; Suzuki and Amaral, 1994), which are a likely the anatomical basis for the functional connections observed in humans (Vincent et al,. 2006; Kahn et al., 2008; Figure 6). Collectively, these anatomical and functional connections define the primate hippocampal-cortical network.

The precise function of the components of the hippocampal-cortical network is not clear and is extensively debated (Gusnard, 2005; Buckner and Carroll, 2007; Hassabis and Maguire, 2007; 2009; Vann et al., 2009; Bar et al., 2009; Schacter et al., 2012). This network contains many of the core components of the so-called default network, which is particularly active during passive vs. engaged task states (Gusnard and Raichle, 2001; Raichle et al., 2001; Buckner et al., 2008). One perspective is that this network underlies different forms of self-projection, including remembering the past, imaging the future, and taking the perspective of others (Buckner and Carroll, 2007). Another perspective suggests that the core function of this network is the generation and maintenance of coherent scenes or events (Hassabis and Maguire, 2007). Notably, all of the hypotheses about the function of this network include the constructive and associative processes underlying episodic memory. Ultimately, it may be necessary to develop a monkey model of the parietal components of the hippocampal-cortical system to understand the

specific contribution of this network to episodic memory (Vincent et al., 2010; Miyamoto et al., 2013).

The Frontoparietal Network

The frontoparietal network is one of the least well understood networks in the human brain. Because of methodological limitations in studying the human brain, human fMRI results are often interpreted in the context of knowledge obtained via invasive methods from non-human primates, such as macaque monkeys. However, the evolutionary divergence of macaques and humans occurred approximately 25 million years ago (Stewart and Disotell, 1998), so the usefulness of a monkey model is limited for some forms of higher brain function. Studies of cortical expansion between monkeys and humans suggest that many of the areas that have undergone the greatest expansion in the primate lineage are located within the frontoparietal network (Ongür et al. 2003; Semendeferi et al., 2001; Van Essen and Dierker, 2007; Hill et al., 2010). In fact, it is unlikely that macaques have a frontoparietal network (Mantini et al., 2013; but see Miyamoto et al., 2013). Compared to the rest of the brain, many regions of the frontoparietal network are structurally immature at birth and undergo a slower, more extensive developmental expansion (Hill et al., 2010). Delayed development will result in relatively greater influence of environment on the structure and function of this network (Brun et al., 2009; Petanjek et al., 2011). Accordingly, it has recently been shown that regions within the frontoparietal network show the greatest individual variability in functional connectivity patterns (Mueller et al., 2013). Understanding the function of the frontoparietal network will likely be key to resolving many puzzles of human cognitive neuroscience, including episodic memory.

Much of what is known about the connectional anatomy of the frontoparietal network comes from studies of functional connectivity. The core nodes of the frontoparietal network include anterior prefrontal cortex, dorsolateral prefrontal cortex, anterior cingulate/medial frontal cortex, lateral cerebellum, anterior insula, caudate, and parietal cortex in and around the intraparietal sulcus (Damoiseaux et al., 2006; Seeley et al., 2007; Dosenbach et al,. 2007; Vincent 2008; Spreng et al., 2010; Yeo et al., 2011). The frontoparietal network is significantly lateralized (Damoiseaux et al., 2006; Vincent et al., 2008). Finally, the frontoparietal network can be divided into two distinct subsystems (Seeley et al., 2007; Dosenbach et al., 2007). The first system includes dorsal anterior cingulate/medial superior frontal cortex, the anterior insula/frontal operculum. The second system includes lateral prefrontal cortex, posterior cingulate, precuneus, and lateral parietal cortex including the intraparietal sulcus. Here, I have focused on the anterior prefrontal and parietal components of this network because of their hypothesized roles in recognition memory.

Functional neuroimaging has long implicated left aPFC in recognition memory, but the precise function has remained elusive. Left aPFC tends to be more activated during hits than correct rejections (Konishi et al., 2000; Kahn et al., 2004; Figure 7). However, as demonstrated by the present behavioral results, the retrieval success contrast is confounded by the fact that old judgments tend to be made with greater confidence than new judgments. When aPFC responses for new and old judgments are matched for retrospective confidence rating, no retrieval success effect is observed in this region (Figure 9). Left aPFC is especially engaged during the retrieval of contextual information during source memory tasks (Nolde et al., 1998; Ranganath and Paller, 1999; 2000; Rugg et al,. 1999; Ranganath et al., 2000; Kahn et al., 2004; Simons et al., 2004; 2005) and lesions to lateral prefrontal cortex can lead to poor performance on source memory

tasks (Janowsky et al., 1989a). However, as demonstrated by Ranganath and colleagues (2000), activation in left aPFC appears to track retrieval demands rather than source memory per se. Specifically, aPFC is more activated by both old and new judgments when the successful task performance relies on recollection of specific details vs. item memory.

Like the aPFC, the functional significance of the dorsal parietal activation has also been elusive. Several event-related fMRI studies of episodic memory have noted functional heterogeneity of the retrieval success effect in parietal cortex (e.g. Henson et al., 1999; Wheeler and Buckner, 2004; Herron et al., 2004; Yonelinas et al., 2005). The ventral posterior parietal cortex (reviewed above) is consistently more activated by contrasts that separated trials of high memory strength from low memory strength using the remember/know procedure, source memory paradigms, and manipulations of encoding. In contrast, the dorsal anterior parietal cortex in and around the intraparietal sulcus is engaged during retrieval success, but not significantly more engaged on trials by the recollection of contextual details (e.g. Wheeler and Buckner 2004; Yonelinas et al., 2005). The present results suggest that alIPS may indicate decision confidence (Figure 9). Consistent with this possibility, neurophysiology studies in monkeys suggest that confidence associated with a decision is represented by the firing rate of parietal neurons (Kiani et al., 2009).

Several recent studies suggest that the aPFC is critical metacognitive processes, including the monitoring and control of memory retrieval processes (Fleming and Dolan, 2012; Shimamura, 2008). Consistent with this account, structural damage to frontal cortex is with poor metacognitive performance on memory tasks (Janowsky et al., 1989b; Souchay et al., 2000; Pannu and Kaszniak, 2005; Pannu et al., 2005). In addition, numerous neuroimaging studies have found associations between activation in prefrontal cortex and feeling-of-knowing or high

retrospective confidence ratings (Kikyo et al., 2002; Maril et al., 2003; 2005; Yonelinas et al., 2005; Elman et al., 2012). Indeed, a recent study of episodic feeling-of-knowing identified a brain network that is highly similar to the frontoparietal network (Elman et al., 2012). Moreover, functional imaging and electrophysiological responses in aPFC tend to have a late onset and temporally extended time course, which is consistent with a role in post-retrieval monitoring (Schacter et al., 1997; Buckner et al., 1998; Düzel et al., 1999). Monitoring and metacognitive awareness may be necessary to implement cognitive control over of information processing and action planning during recognition memory judgments (Fernandez-Duque et al., 2000).

The hippocampal-cortical network and frontoparietal network may then be distinguished by distinct roles in mnemonic vs. evaluative and control processes. In this framework, mnemonic representations are constructed in the hippocampal-cortical network. These percepts are then transferred to the frontoparietal network, which holds the recognized information online in working memory, assesses the strength and relevance of evidence, and uses this information to guide further information processing and action selection. Importantly, the content that can be processed by frontoparietal network does not appear to be restricted to the domain of episodic memory (e.g. Spreng et al., 2010). This model of episodic retrieval predicts that activation of the frontoparietal network would be eliminated if no decision was required. Thus, episodic remembering in the absence of a decision-making requirement should exclusively engage the hippocampal-cortex network.

Conclusions

The present results add to the growing evidence that episodic memory retrieval is supported by two distinct large-scale brain networks (O'Connor et al., 2010; Spreng et al., 2010).

One of these brain networks is correlated with the perception of familiarity and includes the hippocampal formation, ventral posterior inferior parietal lobule, and posterior cingulate cortex. The other brain network is correlated with the retrospective confidence judgments and includes anterior prefrontal cortex and intraparietal sulcus. Within each network, the regional response properties were found to be highly similar, which indicates that future study of episodic memory judgments will benefit from considering the roles of these two pathways. Future studies should focus on identifying the core computations performed by each of these networks. In particular, it will be necessary to understand what information is redundantly represented within the network as well as the unique contributions of each region within the network.

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Appendix 1A: Encoding Instructions

If you have a cell phone or other device that could distract you, please power it off.

In the first set of tasks, you will see words presented on a screen, one at a time. Your task will be to judge whether the word you are seeing is an abstract or a concrete noun. A concrete noun is something you can see, hear, smell, taste, or feel such as "dog" or "table". An abstract noun is something you can't experience with your senses such as "intelligence" or "liberty." You will have 2 s to make the abstract-concrete judgment. Please respond as quickly and accurately as you can. Try and make your best response for each and every word that you see. If you make a mistake, please move on to the next word. You should press one of two buttons to indicate whether the word is abstract or concrete:

Press with your **LEFT index** finger if it is <u>ABSTRACT.</u>

Press with your **RIGHT index** finger if it is <u>CONCRETE.</u>

Lets practice…

Press the LEFT index finger for abstract

RIGHT index finger for concrete,

LEFT for abstract,

RIGHT for concrete,

for concrete, abstract, abstract, concrete, abstract, concrete.

Great.

It is important that you make your response while the word is on the screen. If you enter in your response too late or do not respond at all, this will be recorded as an error and the computer won't record your response. Please make sure to respond as quickly and accurately as you can from the beginning to the end of the task. Do you have any questions?

Appendix 1B: Recognition Instructions

In this part, what we're going to do is test your memory for the words that were presented during the abstract-concrete judgment task.

You will be shown a series of words one at a time. Some of those studied words will be intermixed with some new words. I want you to decide, for each word, whether you recognize the word from earlier or not. We'll call the words that were shown to you earlier "OLD" words. The other words will be words that were not previously shown to you; that is, words that did not appear in the abstract-concrete judgment task. We'll call these items "NEW" words. During the test 50% of the words will be "OLD" and 50% will be "NEW.

The words will be presented one at a time on the computer screen. Your task is simply to watch each word and to decide if the word is OLD (i.e. was presented to you earlier in the abstract-concrete judgment task) or NEW (i.e. it was not among the words presented to you in the abstract-concrete judgment task). When you decide OLD vs. NEW, I also want you to assess your confidence in your OLD-NEW decision on a 3-point scale ranging from 1. LOW CONFIDENCE 2. MODERATE CONFIDENCE and 3. HIGH CONFIDENCE.

Specifically, on this memory test I'd like you to make one of six button responses for each word. You can imagine these 6 responses as a scale going from high confidence to high confidence old.

- **RIGHT RING** finger: if you feel certain the word is **NEW**, in other words you are **HIGHLY CONFIDENT.**
- **RIGHT MIDDLE** finger: if you believe the word is **NEW**, and you are reasonably sure of your choice, in other words you are **MODERATELY CONFIDENT.**

- **RIGHT INDEX** finger: if you believe the word is **NEW**, but you are not sure, in other words you have **LOW CONFIDENCE.**
- **LEFT INDEX** finger: if you believe the word is **OLD**, but you are not sure, in other words you have **LOW CONFIDENCE.**
- **LEFT MIDDLE** finger: if you believe the word is **OLD**, and you are reasonably sure of your choice, in other words you are **MODERATELY CONFIDENT.**
- **LEFT RING** finger: if you feel certain the word is **OLD**, in other words you are **HIGHLY CONFIDENT.**

A highly confident response is one where you specifically remember thoughts that were prompted by the item back when it was presented during the abstract-concrete task. Let me give you an example of a highly confident old response. Let's say that one of the words you saw earlier was "bicycle." You answered "concrete." Afterward you thought about the fact that your brother's birthday is next month and you plan to buy him a bicycle. Later, during the memory task, the word "bicycle" appears. You are certain that this word is old because you remember thinking about your brother when you first saw it during the abstract-concrete task. This type of strong memory where you remember aspects about the experience of seeing the word in the abstract-concrete task would be an example of a "highly confident old" response.

Let me give you an example of a highly confident new response. Let's say that one of the words on the memory task is "Tyrannosaurus Rex." When you see the word, you are absolutely certain that it did not appear in the abstract-concrete task. This type of trial, when you feel a high level of confidence that you don't remember the word from the abstract-concrete task, is an example of a "highly confident new" response.

I also ask that you try to distribute your confidence responses so that you use all of the buttons a few times.

To summarize, you should make a button press with differing hands to indicate your old-new decision:

- **RIGHT** hand if you believe the word is **NEW**.
- **LEFT** hand if you believe the word is **OLD**.

In addition you should press with differing fingers to indicate your confidence in your old-new choice:

- **INDEX** finger if you have **LOW CONFIDENCE** in your old-new choice.
- **MIDDLE** finger if you are **MODERATELY CONFIDENT** in your old-new choice.
- **RING** finger if you are **HIGHLY CONFIDENT** in your old-new choice.

Lets practice…

Press the:

RIGHT RING finger for **HIGH CONFIDENCE NEW**,

LEFT INDEX finger for **LOW CONFIDENCE OLD**,

RIGHT MIDDLE finger for **MODERATE CONFIDENCE NEW**,

LEFT RING finger for **HIGH CONFIDENCE OLD**,

LEFT MIDDLE finger for **MODERATE CONFIDENCE OLD**,

RIGHT INDEX finger for **LOW CONFIDENCE NEW,**

MODERATE CONFIDENCE NEW,

HIGH CONFIDENCE OLD,

LOW CONFIDENCE OLD,

MODERATE CONFIDENCE OLD,

HIGH CONFIDENCE NEW,

LOW CONFIDENCE NEW,

Great.

Thus, to recap, the button presses indicate your decision of whether or not the word is NEW or OLD. If you believe that the item is OLD, press with your **LEFT HAND.** If you believe that the item is NEW, press with your **RIGHT HAND.** If you are HIGHLY CONFIDENT, press with your RING FINGER. If you are MODERATELY CONFIDENT, press with your MIDDLE FINGER. If you are guessing or otherwise have LOW CONFIDENCE in your decision, press with your INDEX FINGER.

You will be able to answer while the word is shown on the screen. It is critical that you make your memory decision prior to the removal of the word. If you have not made your response by the time the word disappears, please just move on to the next item. Please press one key only for each item. Finally, you'll have about 3 s to make your response. Thus, you likely will feel that you have enough time to make this decision while the word is on the screen. Please try to respond as quickly and accurately as possible.

There is one more important aspect to this experiment. You will receive money for each correct response you make. If the presented word is NEW and you respond accurately that it is NEW (regardless of confidence level), you will receive money. Similarly, if the presented word is OLD and you accurately respond that it is OLD (again, regardless of confidence level), you will receive money. The amount of money that you can receive for a correct response, however, will change for each block of trials. At the beginning of each recognition memory trial, you will be presented with a cue that will indicate how much money a correct OLD or NEW decision will

be worth. The cues will be ¢ signs or $ dollar signs, which indicate low and high rewards, respectively.

The value for a correct OLD response will be shown on the RIGHT side of the fixation point. The value for a correct NEW response will be shown on the LEFT side of the fixation point. Notice that the left/right placement of the cues on the screen corresponds to the left/right hand response for old and new items.

On some trials an accurate OLD response will be worth the same as an accurate NEW response. On other trials an accurate NEW response may be worth more than an accurate OLD response or vice versa. The values of an OLD or NEW response are random and are not in any way associated with whether or not the upcoming item actually is OLD or NEW. Each decision will be worth either a low reward (e.g. a few pennies) or a high reward (a larger cash value). A ¢ cue will indicate a low reward. A $ cue will indicate a high reward. The monetary value of your decisions will add up over the course of an hour. You should try to obtain as much money as you can throughout the memory test. Remember, you only get money for accurate responses.

For this experiment, you will receive a payment that will be directly proportional to the amount of money that you accumulate over all trials. All the money that you earn today will come from your performance on these trials.

Now we are going to run a practice test. For this test, I want you to say out loud what the cue indicates as well as your decision. When the cue appears, please say out loud whether a correct OLD response is worth more, a correct NEW response is worth more, or if the responses are worth the same. When the test word appears, please say out loud whether it is OLD or NEW in addition to making your key press decision. During the actual test, you don't need to say

anything out loud. I just want you to say it out loud during the practice test so that I know that you understand the test.

One final aspect of the experiment is worth mentioning. In addition to the memory trials, you will also see a second type of trial that simply consists of the presentation of a black fixation point. Your task is to simply fixate on the black point, and wait for the next word to appear.

Finally, I just want to let you know that the majority of the money you will be making from the experiment today will be from accurate responses to items with high reward values. Therefore, you don't want to not miss a high reward item. Do you have any questions?